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MEAT QUALITIES IN THE SHEEP WITH SPECIAL REFERENCE TO SCOTTISH BREEDS AND CROSSES. II

PART III. COMPARATIVE DEVELOPMENT OF SELECTED INDIVIDUALS OF DIFFERENT BREEDS AND CROSSES AS LAMBS AND HOGGETS

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(With Plates I–XI and Nine Text-figures)

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INTRODUCTION

IN Part II large numbers of individuals of different breeds and crosses have been compared in respect of various carcass measurements. Though these are of value as indices to carcass quality and composition they do not give an accurate quantitative picture of the proportional development of the various tissues of the different parts of the body. One of the main objects of this part of the work is further to elucidate breed differences in respect of these points.

Hammond (1932), by a detailed study of a few individuals of widely different breeds, showed that at a constant age the various types studied differed greatly in their proportional development of different regions of

the body. Many of these differences were of great economic importance, and the results gave an indication of the type of animal most suitable for meat production. The practical application of his results are, however, slightly complicated by the fact that he did not compare the animals at constant weight. Weight rather than age determines price.

The animals used for this investigation are representatives of different breeds and crosses and show a range from relatively unimproved types to animals of excellent conformation and quality. They are all of the same carcass weight, with the further advantage that their ages are approximately the same.

<p style="text-align:center">MATERIAL AND METHODS</p>

The animals used for this investigation have been described in Part I. They were selected so that their external carcass measurements approached as closely as possible the average measurements of the animals of the same breed, age and weight in Part II. Owing to the fact that measurement data could not be obtained for Cheviot lambs, the representative of that breed was selected on a basis of the writer's knowledge of the breed. A lamb carcass from Uruguay and a Southdown × Romney lamb carcass from New Zealand were included in this work. They are of comparable weight and age with the other lambs. The New Zealand lamb was probably older than the other lambs, being a hill-country bred sheep fattened on the lowlands. Unfortunately we have no exact information as to the breeding of the Uruguay lamb. A reference will also be made to a Southdown × Merino lamb from West Australia. Since, however, this was a female and only part of the carcass was available for dissection it is not directly comparable with the other lambs. Carcass measurements of the animals used in this investigation are given in Appendix II. It was impossible to select all the animals so that they were exactly typical of their weight class in every external carcass measurement. However, the deviations from the average of the respective breeds are, in most cases, small and insignificant. Their magnitude can be seen from Appendices II and VI. Carcass weights of 40 lb. for lambs and 60 lb. for hoggets were aimed at, but slight weight differences could not be avoided. Moreover (see Dissection Technique), transport from Edinburgh to Cambridge produced larger losses than expected from hot weight to cold weight due to the high train temperatures, and resulted in all carcasses at dissection weighing less than desired. This, however, has but little effect on the comparative results.

The carcasses were jointed and dissected as described in the previous

Part (p. 554). The weights of each joint and its components are given in Appendix III. The weight of individual bones in the carcass and the constituents of the head are given in Appendices IV and V respectively.

Since bone is the earliest developing tissue in the carcass and muscle growth is dependent on it (Hammond, 1932) we first made a study of the skeletal development. Subsequently we dealt with muscle and fat development. Breed differences are dealt with in § I and changes with increase in age and weight in § II. In § III we study the variation in body proportions and the percentage composition of the total carcass and its various joints in the different breeds and crosses and relate these to the value of the different types of animals for meat production. The proportional development and/or growth of different parts or tissues of the body has been compared in three main ways.

(1) Development of different parts or tissues of the body has been measured by comparison with a standard part or tissue. This has a great advantage in that the comparative results are not affected by other parts. The standard part should preferably be one which does not fluctuate much in size.

(2) The different parts or tissues of the body can be expressed as a percentage of the body weight. Also the constituents of each part can be expressed as a percentage of its total weight. This method has, however, the serious disadvantage, that unless the weights of all the carcasses and their respective parts were constant, the proportions of one part or tissue are affected by changes in others. It is therefore often not clear whether one part is actually small or appears to be so owing to another part being abnormally large. Owing to this fact we have largely refrained from using this method, except in studying the actual composition of the different joints as affecting their value to the butcher.

(3) To study age changes it is useful to express the part or tissue at any age as a percentage of the same part or tissue at a younger age. Therefore we have expressed the weight of different parts and their constituents in the hoggets as a percentage of the same parts and constituents in the lambs.

Our data are not very suitable for growth study as the animals are of two ages only, and the lack of data on lambs at birth makes it impossible to follow the trend of growth up to 4·5 months old. Moreover, the hoggets have not been reared on a level of nutrition comparable to the lambs, so their differences from the lambs cannot be attributed to age changes alone.

The dorsal view of each carcass and cross-section surfaces at the last

rib have been photographed as well as several parts of the skeleton to illustrate the effect of breed and age. The arrangement is identical in all the plates in order to show as well as possible the effect of breed and age.

§ I. BREED DIFFERENCES IN DEVELOPMENT OF BONE, MUSCLE AND FAT

A. SKELETAL DEVELOPMENT

(1) *The actual and relative weights of the different parts of the skeleton*

(a) Actual weights of the skeleton.

The actual weights in grams of the bones in each joint and the total carcass in lambs and hoggets of the different breeds are given in Appendix III. The weights of individual bones in the body are recorded in Appendix IV. From these it is clear that great breed differences in the weights of the skeleton exist at approximately constant age and carcass weight in the lambs. The total weight of bones in the carcass, excluding head and feet, varies from 1782 g. in the Southdown × Romney to 2552 g. in the Oxford × B.L.-Cheviot. The Southdown × Romney is followed in ascending order by the Southdown × B.L.-Cheviot, Blackfaced, Cheviot, B.L. × Blackfaced and the Uruguay. The latter, however, has a slightly lighter carcass than the other lambs, so its skeletal weight is relatively greater than shown by the actual weights. The B.L. × Cheviot, Iceland and B.L. × Iceland do not differ much in skeletal weight but are above the average. The Suffolk × B.L.-Cheviot has the second heaviest skeleton of all the lambs. The order of the breed differences is the same as shown by the average weights of the left fore-cannon in lambs of the different breeds in Part II (see Table 43). The magnitude of these differences is also much the same except in the case of the Iceland, and B.L. × Iceland which have approximately the same skeletal weight. This can be attributed to the fact that the Iceland lamb has slightly longer cannon bones than the average for its weight class, while the opposite is true of the B.L. × Iceland.

In the hoggets the breed differences are also great. The weight of bones in dressed carcass varies from 2900 g. in the B.L. × Blackfaced to 3533 g. in the Suffolk × B.L.-Cheviot. The magnitude of the breed differences in bone weight is unfortunately not exactly the same as estimated in Part II from the weight of the left fore-cannon. This is due to the fact that the B.L. × Cheviot and the Suffolk × B.L.-Cheviot representatives are not quite typical for their corresponding weight classes. The former has slightly shorter and lighter and the latter longer and heavier cannons

than the breed averages of Part II. These comparisons do not give an exact picture of the breed differences owing to slight variations in carcass weight.

(b) *Proportions of each part by comparison with the weight of the cannon bones.*

By expressing the weight of bones in the different regions of the body as a percentage of the weight of the four cannon bones, which develop relatively early in life (Hammond, 1932), one can broadly outline the breed differences in relative development. Further reasons for using the cannon bones as a basis are the facts that they can be obtained without damaging the carcass, are easily cleaned and provide a good measure of the total skeletal weight. The data for lambs and hoggets of the different breeds are given in Table 65. The breed differences in the proportional development of the bones in the head are upset by the fact that some of the breeds have horns. Excluding these we find that in the lambs the Southdown × B.L.-Cheviot, B.L. × Blackfaced and Cheviot have proportionately heavier bones in the head than the B.L. × Cheviot and its crosses with the Suffolk and the Oxford, i.e. the breeds with small cannon bones do not have correspondingly lighter bones in the head. This agrees with Hammond's results (1932) where he found that at 5 months old the Welsh and Southdown (small breeds) had proportionately heavier heads than the Suffolk and Lincoln (large breeds). In the hoggets, however, this rule does not hold, as the Cheviot (small breed with relatively light cannons) has proportionately lighter head bones than the Suffolk cross. This may be explained on the grounds that the Cheviot, as a small breed, has attained a greater proportional development of the earlier developing head at the same carcass weight than the large and later developing breed. In other words, the head bones of the latter have continued growth to a relatively greater extent between $4\frac{1}{2}$ and 13 months. Individuality may also be a factor, the Suffolk × B.L.-Cheviot hogget having an exceptionally large head.

There are great breed differences in the relative weight of the cervical vertebrae in the lambs. The Southdown and Oxford crosses with B.L. × Cheviot, the B.L. × Cheviot and Iceland have proportionately light neck vertebrae, while in the Cheviot, Blackfaced and the Suffolk they are relatively heavy.

In the Southdown cross and the B.L. × Blackfaced the cervical vertebrae are only six in number. This may reduce the weight of these. Breed differences in the hoggets are very small. The proportional weight

Table 65. *Relative proportions of the skeleton in wether sheep of different breeds (parts shown as a percentage of four cannons)*

No.	Breed	Age mo.	Wt. of total skeleton g.	Weight of four cannons g.	Head	Vertebrae Cervical	Thoracic	Lumbar	Sacral	Caudal	Ribs	Sternum	Pelvis	Fore-limbs Above cannon	Below cannon	Hind-limbs Above cannon	Below cannon	Total skeleton cannons	Total skeleton head and feet
								Hoggets											
I	B.L. × Blackfaced	13	3892	195·3	337	141	127	94	45	12	254	54	117	329	38	314	33	1893	1484
II	B.L. × Chev.	13	4061	212·9	299	137	138	98	38	13	228	42	102	317	39	324	34	1808	1436
III	Cheviot	13	3976	198·2	296	139	150	104	46	14	248	51	119	326	39	340	35	1906	1536
IV	Oxford × B.L. Chev.	13	4596	241·8	275	139	119	97	34	9	243	44	105	331	39	331	33	1801	1454
V	Suffolk × B.L.-Chev.	13	4745	253·0	310	140	130	98	37	8	231	40	113	299	38	301	31	1775	1396
								Lambs											
XI	B.L. × Blackfaced	4·5	2977	160·8	299	121	146	103	43	9	205	41	110	293	38	310	34	1752	1380
X	B.L. × Chev.	4·5	3136	174·5	275	115	131	94	37	8	222	45	104	292	36	305	32	1698	1353
XII	Cheviot	4·5	2697	143·3	290	131	135	105	38	10	226	40	105	300	38	331	32	1782	1422
VIII	Oxford × B.L.-Chev.	4·5	3350	201·0	226	111	107	102	35	10	184	39	97	278	37	305	34	1566	1270
VII	Suffolk × B.L.-Chev.	4·5	3192	176·0	263	128	124	112	35	11	202	39	102	294	40	328	36	1714	1374
VI	Southdown × B.L.-Chev.	4·5	2607	141·0	316	111	128	98	37	9	213	43	102	288	37	325	35	1742	1355
IX	Blackfaced	4·5	2798	151·6	342	130	127	110	28	10	206	38	96	286	37	301	34	1745	1333
XV	B.L. × Iceland	4·5	3163	170·0	276	127	137	124	30	9	198	41	110	316	40	314	36	1760	1408
XVI	Iceland	4·5	3254	186·0	296	116	108	89	28	4	178	43	106	289	37	324	32	1649	1284

of the thoracic and lumbar vertebrae is also affected by the variation in number of vertebrae and must be allowed for in comparisons. The thoracic and particularly the lumbar vertebrae are late developing parts of the skeleton. The order of development in the lambs of the different breeds is the same in both regions. B.L. × Iceland, Cheviot, B.L. × Blackfaced, Southdown × B.L.-Cheviot and Suffolk × B.L.-Cheviot are the best developed, while the Oxford × B.L.-Cheviot and the Iceland are decidedly poorer developed, followed by the B.L. × Cheviot. This agrees with Hammond's (1932) results that these vertebrae are relatively heavier in smaller and early developing breeds. The sacral vertebrae are well developed in the B.L. × Blackfaced, Cheviot and Southdown × B.L.-Cheviot, but very poorly developed in the Iceland and the Blackfaced, followed by the B.L. × Iceland. In the Blackfaced the sacral vertebrae were only four in number. The poor development of the sacrum in the breeds mentioned confirms the relative lack of development in these regions which is noticeable in the living animal by the sloping rump and low-set tail, though it is possible that the angle of the pelvis with the vertebral column may also be a factor in this connexion. Kronacher & Hogreve (1936) advance this in explanation of the sloping hams in pigs. In the hoggets the Cheviot has the best developed thoracic, lumbar and sacral vertebrae, followed by the B.L. × Cheviot in respect of the thoracic and lumbar vertebrae. The Oxford and Suffolk crosses have the poorest developed thoracic vertebrae, but the B.L. × Blackfaced has the lightest lumbar vertebrae. The sacrum is lightest in the Oxford cross. This gives a partial answer to an issue raised by Hammond (1932) as to whether the lumbar vertebrae would differ as much in relative weight at 1 year old as at 5 months. If we allow for irregularity in the number of lumbar in the lambs we find that in those breeds which are represented both as lambs and hoggets the differences are much the same at both ages. The Cheviot as the smallest, shortest-boned breed is relatively best developed. The Oxford × B.L.-Cheviot has, however, relatively better developed lumbar vertebrae at 13 months than at 4·5 months, while the opposite is true of the B.L. × Blackfaced. These differences are, however, so slight that they may be safely attributed to individuality rather than difference in general trend.

The sacrum is much better developed in the Cheviot and the B.L. × Blackfaced than in the Oxford cross, while the B.L. × Cheviot and its cross with the Suffolk are in an intermediate position. It must be realized that the system here adopted in comparing the different breeds at constant weight as well as at approximate constant age differs from Ham-

mond's where the animals were compared at constant age regardless of weight. In our case the difference in relative development of the large breeds cannot express itself to the same extent as in the small breeds. The reason for this has already been discussed (Part II).

The pelvis is best developed in the various B.L. crosses, followed by the Iceland and Cheviot, in the lambs. The Oxford × B.L.-Cheviot and Blackfaced have the smallest pelvis. Size and early or late development of the breed appear to have no direct effect on the relative development of the pelvis at 4·5 months. Our results therefore do not confirm Hammond's conclusion that the proportions of the pelvis are greater in early-maturing and small breeds. The factor of individuality may be the reason for this. In the hoggets the proportions of the pelvis appear to be greater in the small-boned breeds (Cheviot and B.L. × Blackfaced) and much smaller in the Oxford. At this age its development appears to be retarded in large-boned animals. This situation thus agrees with Hammond's results.

In the lambs the ribs are relatively heavier in the small breeds (Cheviot, Southdown), but lightest in the large breeds (Oxford × B.L.-Cheviot and Iceland). They are also well developed in a medium-sized rather late-maturing breed such as the B.L. × Cheviot. In hoggets, however, no clear-cut trend is apparent. Similarly in respect to the sternum there does not appear to be any definite order, though the hoggets show some indication of better development in the smaller breeds.

The proportions of the bones of the fore-limb above cannon are greatest in the B.L. × Iceland, Cheviot and Suffolk × B.L.-Cheviot, but lowest in the Oxford × B.L.-Cheviot and the Iceland. In the hind-limb the order is slightly different. The Cheviot, Suffolk and Southdown crosses with the Border Leicester and the Iceland show the greatest relative development, and the Blackfaced, Oxford × B.L.-Cheviot and B.L. × Cheviot the smallest. At 13 months the Oxford × B.L.-Cheviot has the proportionately greatest weight of bone in the fore-limb above cannon, followed by the B.L. × Blackfaced and the Cheviot. The Suffolk has the lowest proportions at this age in both limbs. In the hind-limbs the Cheviot has proportionately heaviest bones followed by the Oxford.

The proportional weight of the bones below cannon in both the fore- and the hind-limb differ but little with breed. The proportions of the total skeleton (less head and feet) expressed as a percentage of the weight of the four cannon bones shows that the breed differences are much less than in the various regions of the body. The fact that one breed has better developed bones in one region is largely counter-balanced by

another breed being relatively better developed in another part of the body. This is why the cannon bones can be used as a satisfactory measure of the weight of the total skeleton. It will, however, be noticed in the lambs that the very long-boned breeds Oxford × B.L.-Cheviot and Iceland have proportionately heavier cannons than the other breeds, while the opposite is true for the Cheviot and Border Leicester × Iceland. Therefore the total weight of the skeleton as estimated from the weight of cannon bones will be slightly overestimated in the former (late-developing) and under-estimated in the latter (early-developing) breeds. In the hoggets the Cheviot has proportionately lighter and the Suffolk cross proportionately heavier cannons than the other breeds.

(c) *Proportions of bone in each joint by comparison with the weight of bone in the neck.*

The neck is the least valuable part of the dressed carcass (see § III and Hammond, 1932). Therefore an animal which is relatively well developed in the more valuable parts as compared with the neck is more desirable for meat production. The weight of the bones in each joint has been expressed as a percentage of the weight of the cervical vertebrae (bone in neck) to show the proportional development of the bones in different regions of the body (see Table 66). As the feet of the New Zealand and Uruguay lambs were not available this method enables us to compare these with the other lambs.

In the lambs the Southdown × B.L.-Cheviot has the greatest proportional development of total skeleton and of bone in each joint as compared with the neck. The comparison is perhaps exaggerated by the fact that in this lamb the cervical vertebrae are only six. If an allowance is made for the variation in number of vertebrae in the thorax and loin we find that all the Border Leicester crosses and the Cheviot have well-developed lumbar and thoracic vertebrae. The bones in the pelvis are particularly well developed in the Border Leicester crosses with the Blackfaced and the Cheviot. The limb bones, on the other hand, are relatively best developed in the Iceland and Oxford × B.L.-Cheviot, the bones of the hind-limbs being outstandingly heavy. The Southdown × Romney has relatively very light bones in all parts of the body as compared with the neck. This may be due to the Romney, since the Southdown itself (see Hammond, 1932) and its cross with the B.L. × Cheviot has very light neck vertebrae. The Uruguay and Iceland have proportionately light trunk bones. The Blackfaced has all parts relatively light, particularly the pelvis bones.

Table 66. *Proportion of bone in each joint expressed as percentage of the weight of bones in the neck (cervical vertebrae)*

Breed	No.	Wt. of bone in neck g.	Head	Shoulders	Thorax	Loin	Pelvis	Legs
			Hoggets					
B.L. × Blackfaced	I	275	239	233	308	67	123	222
B.L. × Cheviot	II	291	219	232	298	71	112	237
Cheviot	III	276	213	234	323	75	128	244
Oxford × B.L. Chev.	IV	337	198	238	292	70	107	237
Suffolk × B.L. Chev.	V	353	222	217	288	70	113	216
			Lambs					
B.L. × Blackfaced	XI	195	247	242	322	85	133	256
B.L. × Cheviot	X	200	240	254	346	82	130	266
Cheviot	XII	188	221	229	306	80	117	252
Oxford × B.L. Chev.	VIII	223	204	251	298	92	129	275
Suffolk × B.L. Chev.	VII	226	204	229	284	87	115	255
Southdown × B.L. Chev.	VI	157	283	258	245	88	133	292
Blackfaced	IX	197	263	220	285	85	104	232
Uruguay	XIII	216	---	224	271	76	113	245
Southdown × Romney	XIV	192	---	197	264	57	103	207
B.L. × Iceland	XV	216	217	249	296	98	118	247
Iceland	XVI	215	256	250	284	77	120	280

At 13 months the Cheviot has proportionately heavier bones in all parts, with the exception of the shoulders and head, than the other breeds. The B.L. × Blackfaced has well-developed bones in the thorax and pelvis but has relatively light bones in the hind-limbs. The B.L. × Cheviot is in an intermediate position. The Oxford cross has relatively very heavy limb bones, while the opposite is true of the Suffolk cross. It is striking that the bones of the hind-limb are relatively much heavier than the bones of the fore-limb at both ages in the Cheviot and in the Iceland lamb, while in the Blackfaced and in all the Border Leicester crosses this difference is much less marked.

(2) *The length, shape and weight of individual bones*

Breed differences in weight of the bones in the various regions of the body can be largely explained by differences in the shape of the individual bones. This is compared by photographs and measurements. All photographs are taken on a centimetre squared background. This enables one to measure the actual as well as relative size of the bones. In some plates bones from the Southdown lamb of 5 months old (No. XIII from Hammond, 1932) are included and marked *S*.

(a) *The skull.*

Table 67 and Pl. I illustrate the breed differences and age changes in the skull. At 4·5 months the Oxford × B.L.-Cheviot has the longest skull, closely followed by the B.L. × Cheviot and the Suffolk × B.L.-Cheviot.

Table 67. *Measurement of the skull*

No.	Breed	Actual length mm.	Actual width mm. outer	Actual width mm. inner	Width at eyes as percentage of length	
					Outside top of eye orbit	Inside bottom of eye orbit
	Hoggets					
I	B.L. × Blackfaced	231	119	84	51·5	36·4
II	B.L. × Chev.	235	117	82	49·7	34·9
III	Cheviot	230	118	80	51·3	34·8
IV	Oxford × B.L.-Chev.	240	124	85	51·7	35·4
V	Suffolk × B.L.-Chev.	245	121	85	49·3	34·7
	Lambs					
XI	B.L. × Blackfaced	198	110	77	55·5	38·9
X	B.L. × Chev.	210	113	81	53·8	38·5
XII	Cheviot	195	105	76	53·8	38·9
VIII	Oxford × B.L.-Chev.	211	111	78	52·6	37·0
VII	Suffolk × B.L.-Chev.	208	109	81	52·5	38·9
VI	Southdown × B.L.-Chev.	199	107	77	53·8	38·7
IX	Blackfaced	201	111	75	55·2	37·3
XIII	Uruguay	—	—	—	—	—
XIV	Southdown × Romney	—	—	—		
XV	B.L. × Iceland	204	108	78	52·9	38·2
XVI	Iceland	199	111	80	55·8	40·0

Table 68 *Measurements of the sixth ribs*

No.	Breed	Actual length mm.	Percentage of length	
			Spring	Width
	Hoggets			
I	B.L. × Blackfaced	163	24·5	12·9
II	B.L. × Chev.	162	24·7	12·3
III	Cheviot	163	22·1	12·9
IV	Oxford × B.L.-Chev.	152	28·3	15·1
V	Suffolk × B.L.-Chev.	160	27·5	12·5
	Lambs			
XI	B.L. × Blackfaced	135	28·2	11·1
X	B.L. × Chev.	150	25·3	10·0
XII	Cheviot	130	29·2	10·8
VIII	Oxford × B.L.-Chev.	145	25·5	11·7
VII	Suffolk × B.L.-Chev.	147	25·8	12·2
VI	Southdown × B.L.-Chev.	131	28·2	12·2
IX	Blackfaced	136	27·2	11·0
XIII	Uruguay	149	22·2	11·4
XIV	Southdown × Romney	140	25·0	10·7
XV	B.L. × Iceland	140	29·3	10·0
XVI	Iceland	157	25·5	10·8

The other breeds show little difference and are about 10–15 mm. shorter than the Oxford × B.L.-Cheviot. The Cheviot followed by the Southdown (S) has the shortest skull. The Southdown cross with the B.L. × Cheviot has a skull of intermediate length compared with the parent breeds, but it approaches more the Southdown. There appears to be definite correlation between the length of the cannon bones and length of skull (see Tables 67 and 69 and Pls. I and II). In the hoggets the Cheviot and B.L. × Blackfaced have the shortest skulls, followed by the B.L. × Cheviot, Oxford × B.L.-Cheviot and the Suffolk × B.L.-Cheviot which has 15 mm. longer skull than the Cheviot. This is the same order as for the length of the cannon bones. There is much less breed difference in the actual width of the skull than its length. The width measurements have been expressed as a percentage of the length, which gives a good measure of the relative width of the skull. In the lambs the skull is widest in the horned breeds. This is possibly due to the greater development of the frontals in the horned breeds. The skull is relatively narrowest in the large breeds (Suffolk and Oxford crosses). At 13 months there is still less breed difference in the relative width of the skulls. The large breeds have attained as great development in the width as the smaller breeds at this age. There is an increase from about 30-40 mm. in the length of the skull with increase in age from 4·5 to 13 months and 50% carcass weight increase. Length has increased proportionately more with age and weight, since the latter as a percentage of the former is higher in the lambs in all cases. Hammond (1932) in sheep, and Berger (1920) in cattle, record the same result.

(b) The cannons.

Table 69 shows the breed differences in length, weight and thickness in the fore- and hind-cannons. Pl. II illustrates the breed differences and age changes in the form of the left fore-cannon, and Pl. III in the left hind-cannons. The breed differences in the length of fore-cannon are marked and are in the same order as was found to be the case in Part II. However, the Iceland has rather longer cannon and the B.L. × Iceland shorter than the average for their respective weight classes. Of the two additional breeds included here the Southdown (S) has the shortest cannon of all and the Cheviot is but slightly longer. The breed differences in minimum circumference are not so great. The absolute measure of minimum circumference does not give the best picture of the difference in the thickness of the shaft, as a short bone with the same circumference as another longer is relatively much thicker. Therefore we have expressed

Table 69. *Measurements and weights of common bones (average of both sides)*

No.	Breed	Fore			Percentage of length		Hind			Percentage of length	
		Length mm.	Min. circumference	Weight g.	Circumference	Weight	Length mm.	Min. circumference	Weight g.	Circumference	Weight
	Hoggets										
I	B.L. × Blackfaced	127	49	47·6	38·6	37·4	135	48	50·0	35·5	37·0
II	B.L. × Chev.	129	50	53·0	38·8	41·1	139	49	53·3	35·2	38·3
III	Cheviot	123·5	50	49·0	40·5	39·7	130	48	50·0	36·9	38·5
IV	Oxford × B.L.-Chev.	132·5	55	61·0	41·5	46·0	137	53	60·0	38·7	43·8
V	Suffolk × B.L.-Chev.	133	57	63·0	42·8	47·4	141	53	63·5	37·6	45·0
	Lambs										
XI	B.L. × Blackfaced	114·5	45	39·0	39·3	34·1	123	44	41·4	35·8	33·6
X	B.L. × Chev.	122	47	43·1	38·5	35·3	128	45	44·0	35·1	34·3
XII	Cheviot	107	45	36·0	42·0	33·6	111	43	35·6	38·7	32·1
VIII	Oxford × B.L.-Chev.	123	46·5	49·0	37·8	39·8	131	45	51·5	34·4	39·3
VII	Suffolk × B.L.-Chev.	113·5	45	42·5	39·6	37·4	123	45	45·5	36·6	37·0
VI	Southdown × B.L.-Chev.	106	44	34·5	41·5	32·5	112	43	36·0	38·4	32·1
IX	Blackfaced	110·5	47·5	37·8	43·0	34·2	117	44·5	38·0	38·0	32·5
XV	B.L. × Iceland	117	46	42·0	39·3	35·9	125	44	43·0	35·2	34·4
XVI	Iceland	132·5	45	45·0	34·0	33·9	140	45	48·0	32·1	34·3

the minimum circumference as a percentage of the length, which is a good relative measure of the slimness of the shaft. When the minimum circumference as a percentage of the length is compared with the weight of the bone as a percentage of the length, one gets a good picture of the shape of the bone. The weight : length ratio as referred to in Part II gives the best readily obtainable measure of the average thickness of the bone. In Part II it was shown that the relative difference in weight : length ratio was much greater than the relative difference in the minimum circumference in the Oxford cross as compared with the Southdown cross. This was explained by the relatively coarse extremities on the Oxford cross cannons. This condition is also obvious from Pl. II and Table 69. In lamb No. VIII the minimum circumference as a percentage of the cannon is relatively low, but the weight : length ratio higher than in all other lambs. This is also noticeable in lamb No. VII and to less extent in No. X. Contrary to this are lambs Nos. VI, IX and XII, all of which have large circumferences as a percentage of the cannon length, and low weight : length ratios. It will also be noticed that the latter group of lambs are much better developed in respect of muscle and fat and have generally shorter and lighter bones and better conformation than the former group. Therefore a relatively short cannon with a thick shaft but relatively fine and light extremities (as Nos. VI, XII, IX and XI in Pl. II) appears to be associated with early maturity and desirable carcass quality, while long bones with a slender shaft but coarse and heavy extremities (Nos. VIII, X and XVI) (Pl. II) are indicative of late development and inferior meat quality. Hammond (1932) found that in semi-wild breeds (Soay and Shetland) thickness growth in bones was inhibited as compared with the improved mutton breeds (Hampshire and Suffolk), while the wool-type Merino was intermediate. Hammond (1937b) states that the two different forms of bone growth (length and thickness growth) are independent and that to some extent one can be affected without the other, and it is fairly certain that in the improvement of breeds for mutton qualities thickness growth has been affected to a much greater extent than length growth. He also quotes Nathusius (1880) who found that early maturing breeds (Southdown) had short broad skulls and late maturing breeds (Merino) long ones. "That is, increase in the factors for bone length growth is not concerned in the improvement of mutton qualities, but rather the contrary; improvements, however, are associated with the increase in the factors for bone thickness." As thickness of bone increases the skeletal weight the latter is unfortunate. Our results agree in the main with the above statements. We, however, find that the

weight of the skeleton can be actually decreased with breed improvements, i.e. both by shortening the bones as well as reducing the coarseness of the extremities of the long bones. The increase in the thickness of the long bones, which follows breed improvement, appears to be only associated with the shaft. The slim bones of the Iceland breed confirms Hammond's results that thickness growth is inhibited in semi-wild as compared with improved breeds. In the hoggets it is clear that the Suffolk × B.L.-Cheviot as well as the Oxford × B.L.-Cheviot attain relatively good development in minimum circumference of cannon with age. Therefore the slimness of the shaft of their cannons as lambs (particularly in the case of the former) appears chiefly to be due to the large size of these breeds rather than very late maturity. Nevertheless, they are unfit for slaughter at light weights. The percentage increase in length and minimum circumference with age and weight is much the same, but weight increase is much greater.

The breed differences and age changes in the hind-cannon follow the same general trend as in the fore-cannon. The hind-cannons are absolutely longer and in most cases have absolutely smaller minimum circumferences. The breed differences in their circumference is less pronounced than in the fore-cannons. The weight per unit length is in most cases less than in the fore-cannons.

(c) *The femur.*

(Femurs are compared in Table 70 and Pl. IV.) The Southdown × Romney has the shortest femur, followed by the Cheviot. Southdown ×

Table 70. *Measurements of femur*

No.	Breed	Length mm.	Circumference mm.	Percentage of length Circumference	Percentage of length Weight
			Hoggets		
I	B.L. × Blackfaced	180	61	33·9	76·9
II	B.L. × Chev.	189	61	32·3	83·0
III	Cheviot	175	61	34·9	87·1
IV	Oxford × B.L.-Chev.	194	66	34·0	93·0
V	Suffolk × B.L.-Chev.	181	66	36·5	93·0
			Lambs		
XI	B.L. × Blackfaced	167	55	32·9	70·0
X	B.L. × Chev.	168	60	35·7	73·5
XII	Cheviot	155	57	36·7	72·9
VIII	Oxford × B.L.-Chev.	170	58	34·1	82·9
VII	Suffolk × B.L.-Chev.	168	61	36·3	81·0
VI	Southdown × B.L.-Chev.	156	58	37·2	68·3
IX	Blackfaced	160	52	32·5	64·7
XIII	Uruguay	165	56	33·9	72·7
XIV	Southdown × Romney	146	52	35·6	63·4
XV	B.L. × Iceland	163	56	34·3	77·3
XVI	Iceland	179	58	32·4	77·7

B.L.-Cheviot and the Blackfaced. The Border Leicester crosses, the Uruguay and Suffolk × B.L.-Cheviot have practically the same femur length, followed by the Oxford × B.L.-Cheviot. The Iceland has the longest femur. There is a considerable difference in the minimum circumference. The Southdown × B.L.-Cheviot, followed by the Cheviot, Suffolk × B.L.-Cheviot and Southdown × Romney, have the relatively thickest femurs as measured by the minimum circumference compared with the length. The Iceland, Blackfaced and B.L. × Blackfaced have the most slender femur, and the Oxford cross is intermediate. The latter, however, as is the case of the cannon, has proportionately the heaviest femur (greatest weight per unit length) followed by the Suffolk cross. The lowest weight : length ratio of the femur is again met with in the Southdown crosses and the Blackfaced. This shows again that in all the earliest developing and best quality carcasses the minimum circumference is (as percentage of the length) relatively greater as compared with the weight : length ratio, indicating that the best shape of bone is one with thick shaft as compared with the extremities. In the hoggets the breed differences are great. The Cheviot and B.L. × Blackfaced have the shortest femur and the Oxford cross the longest. The proportions are again worst in the Oxford cross. As in the cannon the thickness, as measured by the weight per unit length, has increased more than the length. It will be noticed that there appears to be a positive correlation between the length of femur and leg length (*F*), indicating that long bones are undesirable from the carcass quality point of view.

Table 71. *Measurement of pelvis*

No.	Breed	Actual length mm.	Actual width mm.	Width as percentage of length
	Hoggets			
I	B.L. × Blackfaced	193	91	47·2
II	B.L. × Chev.	198	100	50·5
III	Cheviot	193	98	50·8
IV	Oxford × B.L.-Chev.	202	103	51·0
V	Suffolk × B.L.-Chev.	195	97	49·7
	Lambs			
XI	B.L. × Blackfaced	175	91	52·0
X	B.L. × Chev.	181	86	47·5
XII	Cheviot	166	87	52·4
VIII	Oxford × B.L.-Chev.	179	85	47·5
VII	Suffolk × B.L.-Chev.	173	91	52·6
VI	Southdown × B.L.-Chev.	168	84	50·0
IX	Blackfaced	174	88	50·6
XIII	Uruguay	179	89	49·7
XIV	Southdown × Romney	165	86	52·1
XV	B.L. × Iceland	174	87	50·0
XVI	Iceland	194	88	45·5

(d) *The pelvis.*

Measurements of the pelvis are given in Table 71. The length was measured as illustrated by Hammond (the greatest length of the ilium + ischium, excluding the cartilage). The width was measured point to point from the outer edge of the acetabulum cavity at the junction of the ilium and ischium by callipers. The breeds follow in the main the same trend in pelvis length as for femurs and cannons (Pl. V). The width as a percentage of the length behaves inversely, being greatest in the Cheviot, the Southdown crosses, Suffolk × B.L.-Cheviot and B.L. × Blackfaced. The Iceland has relatively narrowest pelvis, followed by the Oxford × B.L.-Cheviot. At 13 months the Cheviot and the B.L. × Blackfaced have the shortest pelvis and the Oxford cross the longest. The breeds differ but little in relative width except that the B.L. × Blackfaced has the narrower pelvis, which is possibly due to individuality. The width has not increased more than the length with age.

A relatively wide pelvis is desirable from the point of view of conformation, as it necessarily leads to wider hindquarters. It must be realized that the width measurement of the pelvis is not an actual measure of bone thickness. It is more a measure of the length of the pubis combined with the thickness of the ischium at its anterior end. From the above it appears therefore that the length growth of the pubis is not directly correlated with the length growth of the ilium and ischium as some of the shortest pelves are relatively widest.

(e) *The ribs.*

The measurements of the sixth rib are given in Table 68 and these are illustrated in Pl. VI.

The length has been taken as the shortest distance between the extreme ends. The spring of rib is measured by the greatest distance between this line and the side of the rib (see Hammond, 1932, p. 200). The width of rib is the greatest distance from the anterior to the posterior edge of the rib measured by callipers. In the lambs the Cheviot and Southdown × B.L.-Cheviot have the shortest rib, followed by the B.L. × Blackfaced and Blackfaced. The Iceland has the longest rib and the B.L. × Cheviot and its cross with the Suffolk slightly shorter. The Cheviot and B.L. × Iceland have the best sprung ribs, followed by the B.L. × Blackfaced, Southdown × B.L.-Cheviot and Blackfaced. The Uruguay, Oxford × B.L.-Cheviot, B.L. × Cheviot and Iceland followed by the Suffolk cross have the least spring of ribs. This agrees with Hammond's results (1932) which showed that the early maturing breeds had better

sprung ribs than the late-maturing ones. In the hoggets the Oxford ×
B.L.-Cheviot has the shortest rib. The spring follows an opposite trend,
being greatest in the large breeds (Oxford and Suffolk crosses). The length
has increased greatly from 4·3 to 13 months, but the relative spring of the
rib has decreased in the smaller breeds but increased greatly in the larger
ones. There is but little breed difference in relative width of the ribs. In
the lambs the Southdown and Suffolk crosses with the B.L. × Cheviot
have the proportionately widest ribs, but the B.L. crosses with the Cheviot
and Iceland the narrowest. With age the width of rib increases pro-
portionately more than its length. In the hoggets the Oxford cross has
very wide ribs. It should be realized that the spring of rib in the live
animal is not quite the same as that measured here by the curvature of
the rib itself. In the living animal the ribs are held in place by muscles
which affect the spring of the ribs. We find that there is a correlation of
$+0·8192$ between the spring of rib as a percentage of its length and depth
of eye muscle (B) and a correlation of $+0·6844$ between the spring and
shape index of eye muscle ($B/A \times 100$) in the 11 lambs. There is not a
significant correlation between length of rib and length of eye muscle,
being only $+0·2294$. From Appendix II and Table 68 it is clear that there
is a correlation between depth of thorax and length of rib. This points
to the possibility of improving the muscular development by selecting
for relative shallow thorax with well-sprung ribs.

Table 72. *Number of sheep showing variation in rib number*

Breed	Total no. of indi- viduals	Number of ribs on right and left side							
		R. L. 12–12	R. L. 12–13	R. L. 13–12	R. L. 13–13	R. L. 13–14	R. L. 14–13	R. L. 14–14	R. L. 14–12
Iceland	49	2	- -	-	47	--	-	---	---
B.L. × Iceland	40	—	---	—	40	—	---	--	---
Blackfaced	12	---	--	---	12	- -	—	--	--
B.L. × Blackfaced	141	1	1	- -	124	3	1	11	—
Cheviot	53	15	—	1	33	1	3	—	—
B.L. × Cheviot	249	9	1	—	225	5	—	9	—
Southdown × B.L.-Chev.	75	3	1	--	65	1	1	3	1
Oxford × B.L.-Chev.	204	7	4	1	175	5	—	11	1
Suffolk × B.L.-Chev.	192	3	1	—	168	3	4	13	—
Suffolk	98	1	—	-	76	4	4	13	—
Total for all breeds	1113	41	8	2	965	22	13	60	2

(3) *Variation in number of bones in different parts of the skeleton*

It is well known that in several species of animals the number of ribs
varies. Shaw (1929–30) found in the pig from 13 to 17 pairs of ribs.
McMeekan (1938) has also found in closely inbred strains 14–17, and
Berge (1936) in Norway in the Landrace found from 13 to 16 pairs.

Hammond (1932) found Suffolk sheep with 14 pairs of ribs instead of the usual 13. Nathusius (1880) states that the number of ribs in sheep is usually 13 but occasionally may be 12. Table 72 shows the variation in rib number in 1113 sheep of various breeds which we have examined. 85·8 % of the total number of sheep have 13 pairs of ribs. The incidence of 14 pairs is more commonly met with than 12 pairs. An extra rib on one side is not uncommon. Twelve ribs on one side and 14 on the other were found in only two cases. There are considerable breed differences in the variation in rib numbers. All the animals of the Blackfaced and B.L. × Iceland had the normal number 13. Only 4 % of the Iceland had 12 ribs, the remainder 13. The incidence of 12 ribs was most common in the Cheviot, 30 % of the animals studied having 12 pairs of ribs only and none 14 ribs on both sides. The incidence of 14 pairs of ribs was most common in the Suffolk, followed by the Suffolk × B.L.-Cheviot. Only one Suffolk sheep had 12 pairs of ribs. It will be noticed that the large breeds or crosses have more commonly the extra pair of ribs than the smaller breeds.

Variations in number of vertebrae are said to occur most commonly at the junction of the thoracic and lumbar vertebrae. The number of cervical vertebrae is said to be so remarkably constant that it is used as the second most important characteristic differentiating mammals from other vertebrates. In the animals dissected variation in number of

Table 73. *Variation in number of vertebrae and ribs in sheep*

No.	Breed	Vertebrae					Ribs	
		Cervical	Thoracic	Lumbar	Sacral	Caudal	Right	Left
XI	B.L. × Blackfaced	6	14	6	5	14	14	14
I	B.L. × Blackfaced	7	13	6	5	9	13	13
X	B.L. × Cheviot	7	14	6	5	7	14	14
II	B.L. > Cheviot	7	13	6	5	9	13	13
XII	Cheviot	7	13	6	5	9	13	13
III	Cheviot	7	14	6	5	12	13	14
VIII	Oxford × B.L.-Chev.	7	13	7	5	9	13	13
IV	Oxford × B.L.-Chev.	7	13	6	5	7	13	13
VII	Suffolk × B.L.-Chev.	7	13	7	4	8	13	13
V	Suffolk × B.L.-Chev.	7	14	6	5	6	11	14
VI	Southdown × B.L.-Chev.	6	13	6	5	7	13	13
IX	Blackfaced	7	13	7	4	10	13	13
XIII	Uruguay	7	13	6	5	5	13	13
XIV	Southdown × Romney	7	13	5	5	5	13	12
XV	B.L. × Iceland	7	13	7	5	17	13	13
XVI	Iceland	7	13	6	5	11	13	13
XVII	Southdown × Merino	6	13	6	5	—	13	13

vertebrae in all the regions was met with (see Table 73). It can be seen from these that all variations do not necessarily originate at the thoracic-lumbar junction. Two lambs, Nos. VII and IX, had only four sacral

vertebrae but seven lumbar, and in one of these cases (IX) it is obvious that the last lumbar vertebrae is different in form from a normal last lumbar, it being intermediate in shape to a first sacral and last lumbar (see Pl. VII). Therefore it is likely that a lumbarization of the first sacral has taken place. In man sacralization of the last lumbar vertebrae is much more common than lumbarization of the first sacral (Harris, 1938). In two other lambs, Nos. VIII and XV, seven lumbar vertebrae were found and the number in other regions was normal. Hammond (1932) found seven lumbar vertebrae in one Lincoln and one Suffolk wether. In one lamb (XIV) only five lumbar vertebrae were found. It however had only one rib on one side of the last thoracic vertebrae, indicating a partial modification of the first lumbar into a thoracic vertebrae. The remaining thoracic vertebrae were only 12; the sacral and cervical were normal. In this work we classify as thoracic vertebrae all those bearing a rib. In four sheep (III, V, X and XI) 14 thoracic vertebrae are met with. In three of these there was a normal number in the other regions, but in one (XI) a cervical vertebrae was missing. In Nos. VI and XVII, also, only six cervical vertebrae were found with the normal number in other regions. It will be noticed that these are both Southdown crosses, which has a very short neck. After this discovery of six cervical vertebrae in the Southdown × B.L.-Cheviot the neck vertebrae in eight lambs of the same cross were counted by splitting the neck. In five of these only six cervical vertebrae were met with and only 13 thoracic. The vertebral columns showing irregularity in number of vertebrae were examined and X-rayed by Prof. H. A. Harris of the Anatomy School, Cambridge, who confirmed that the first thoracic vertebrae in two lambs with six cervical vertebrae (VI and XI) were structurally typical normal thoracic vertebrae. Following our demonstration of the point, Prof. Harris in X-ray photographs of sheep embryos (Welsh crosses) found two having only six cervical vertebrae and the first thoracic being structurally normal with a pair of well-developed ribs. In man a rudimentary cervical rib is sometimes found (Harris, 1938). The normal number and order of the vertebrae is illustrated by the formula $C_7 T_{13} L_6 S_5$, the total being 31. In only six of the 17 animals dissected was the right number met with in all regions. In three others the total number was the same. In three only 30 vertebrae were found, while five had 32 vertebrae. Deviations from the normal formula are not only due to regional displacement, since the total number varies. Whether this variation is evolutionary or takes place by sudden mutation it is impossible to say without experimentation. These variations are of great economic importance. As illustrated in Plate VII it is obvious

that the total length of the loin is increased by addition and decreased by loss of a vertebrae. As the loin is the most valuable part of the body an increase in its length is of great importance from the butcher's point of view. An extra thoracic vertebrae is also desirable though less so than an extra lumbar. On the other hand it is an advantage to shorten the neck by reduction of vertebrae, as this is the cheapest joint in the carcass. The ideal would be an animal with six cervical, 14 thoracic, seven lumbar and five sacral, provided such an alteration in the body structure would not affect the constitution of the animal. From the breeder's point of view it would be of interest to acquire knowledge of how these variations in bone number are inherited and evolved. This is a problem for the geneticist, which if it could be successfully solved would greatly benefit the meat producer.

B. Muscle development

(1) *Relative weight of muscle in different joints*

The actual weight of muscle in each joint and the total carcass of lambs and hoggets is given in Appendix III. It is obvious that important breed differences exist. As the value of a joint is more dependent on the proportions of muscle to bone and fat to muscle than the actual weight of the latter and the value of the carcass depends greatly on the proportions of the more valuable joints compared with the cheaper ones, muscular development is dealt with under the following headings. (*a*) The weight of muscle in each joint as a percentage of the weight of the bone and (*b*) the proportions of muscle in each joint as a percentage of the muscle in the neck.

(*a*) *Weight of muscle in each joint as a percentage of the weight of bone.*

In Text-figs. 11-17 and Table 74 the weight of muscle as a percentage of the weight of the bones in each joint is illustrated. From these histograms the breed differences in order of merit are clearly illustrated as well as the relative amount of muscle to bone in different joints. The muscle : bone ratio is lowest in the thorax followed closely by the neck and pelvis. The loin followed by the legs have the highest muscle : bone ratio. The shoulders have approximately the same amount of muscle relative to bone as the total carcass. The extent of these differences in the proportions of muscle to bone in the different joints is very great. The weight of muscle in the thorax is only just over three times that of the bone, while in the loin it is more than 6·5 times. This shows clearly the reason for a higher price per lb. of the loin and legs than the thorax or

Text-fig, 11.

Text-fig. 12.

Table 74. *Weight of muscle and fat in different joints shown as a percentage of the weight of the bone (grams)*

Breed		B.L.× Blackfaced		B.L.× Cheviot		Cheviot		Oxford× B.L.-Chev.		Suffolk× B.L.-Chev.		Southdown× B.L. Chev.	Black-faced	Uruguay	Southdown× Romney	B.L.× Iceland	Iceland	Southdown× Merino
Age (months)		4·5	13	4·5	13	4·5	13	4·5	13	4·5	13	4·5	4·5	4·5	4·5	4·5	4·5	4·5
No.		XI	I	X	II	XII	III	VIII	IV	VII	V	VI	IX	XIII	XIV	XV	XVI	XVII
Sex		♂	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂	♀
Joint																		
Neck:	Muscle	346	346	444	397	396	405	321	365	392	333	387	328	299	390	347	447	—
	Fat	256	218	262	166	238	270	201	200	204	184	223	273	268	412	185	207	—
Thorax:	Muscle	335	308	322	365	364	319	281	288	347	301	372	320	292	365	322	340	—
	Fat	228	297	179	239	239	278	219	196	198	241	248	249	278	418	198	188	—
Shoulders:	Muscle	400	478	390	525	470	486	365	418	421	484	513	424	354	468	378	357	500
	Fat	131	251	113	199	173	233	156	151	127	198	219	181	138	292	117	87	225
Loin:	Muscle	645	818	639	891	685	774	565	666	778	725	921	642	501	902	602	673	—
	Fat	369	666	312	438	373	558	308	244	312	478	451	423	376	803	279	299	—
Pelvis:	Muscle	313	409	313	470	420	372	299	407	277	371	459	340	274	311	337	392	—
	Fat	257	393	217	339	265	350	220	246	162	272	339	278	295	388	220	239	—
Legs:	Muscle	536	535	517	536	532	521	417	468	492	548	556	522	450	589	488	422	599
	Fat	134	164	111	130	123	162	104	108	91	127	146	146	104	255	96	69	175
Total carcass:	Muscle	416	441	412	499	458	444	361	404	423	434	497	418	357	467	400	403	—
	Fat	203	286	170	223	211	270	183	174	163	221	240	231	214	374	165	150	—

Muscle and fat as % of weight of bone
Shoulders

Muscle   Fat

Text-fig. 13.

Muscle and fat as % of weight of bone
Pelvis

Muscle   Fat

Text-fig. 14.

neck, quite apart from associated difference in the quality of the muscle. It is striking that the variation between breeds is much greater in the loin and pelvis (late-developing joints) than in the thorax, neck and the total carcass. The fact that the breed differences in the muscle : bone ratio are much less in the total carcass than in most of the individual joints shows that the order of merit varies in the different joints.

Neck. In the neck the Iceland and B.L. × Cheviot have the highest muscle : bone ratio and the Uruguay and the Oxford × B.L.-Cheviot the
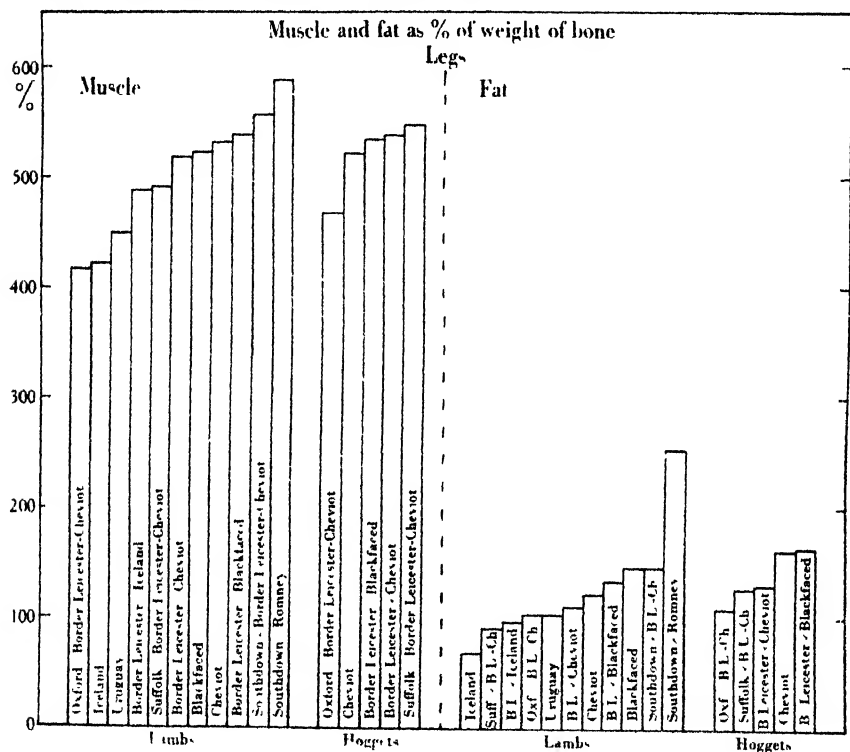
Text-fig. 15.

lowest (see Text-fig. 11); the former having 4·5 times more muscle than bone in this joint and the latter only about three times. In the hoggets the Cheviot has the relatively most muscle in the neck. It will be noticed that the order of merit is very different in the most valuable joints (loin, legs). Therefore one cannot necessarily consider the animals which have relatively best proportions in the neck as yielding carcasses of most desirable quality.

Thorax. In the thorax the breed differences are but small (see Text-fig. 12). The Southdown crosses have the highest muscle : bone ratio and the Iceland and B.L. × Cheviot are in an intermediate position.

Shoulders. The Southdown × B.L.-Cheviot has the highest muscle weight as a percentage of the bone or five times the weight of the latter (see Text-fig. 13). It is followed by the Cheviot and Southdown × Romney.
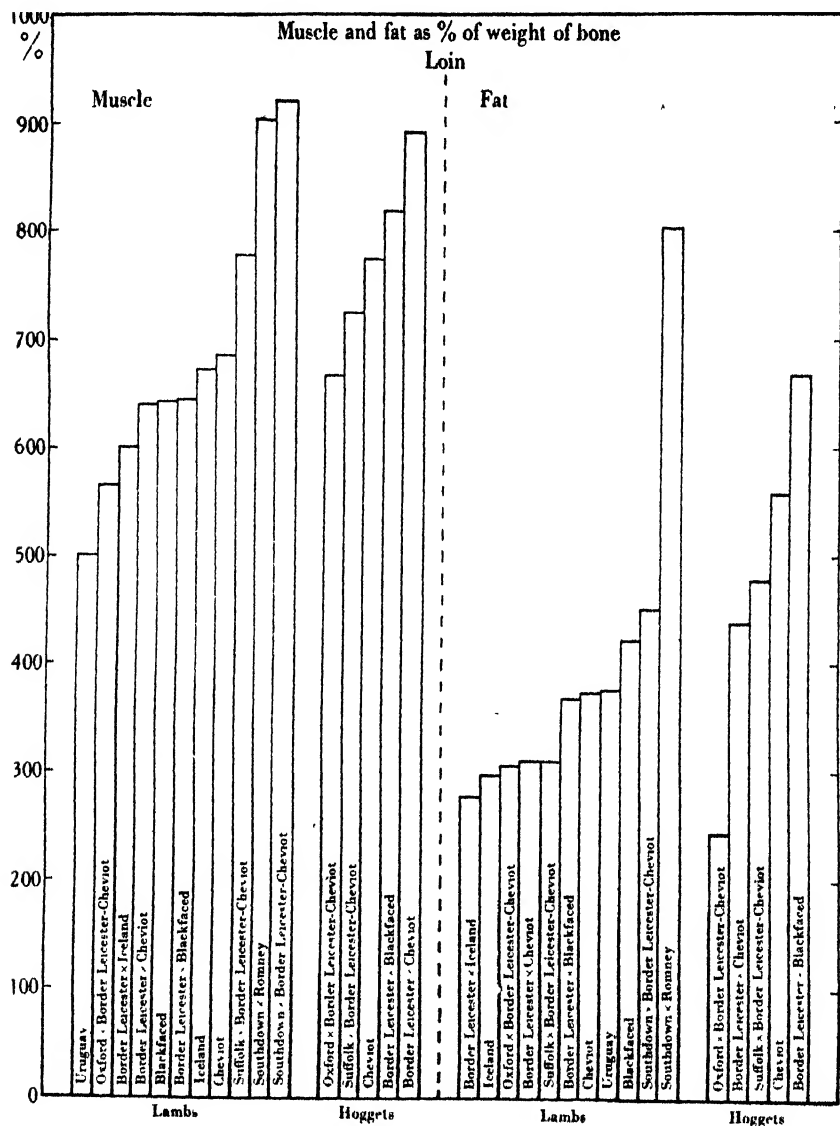
Text-fig. 16.

The Uruguay, Iceland and Oxford × B.L.-Cheviot have the lowest muscle: bone ratio or only 3·5 times the weight of the latter. In the hoggets the B.L. × Cheviot is the best in this respect but the Oxford cross poorest.

Legs. In the legs the order of merit is very similar to that in shoulders,

with the breed differences slightly greater. The muscle in the Southdown ×
Romney being about 600% of the weight of the bone and in the Oxford ×
B.L.-Cheviot only 420% (see Text-fig. 13). In the hoggets the Oxford
cross has the lowest muscle : bone ratio, the other breeds differing but
slightly.

Pelvis. In the pelvis the order of merit is different (see Text-fig. 14).
The Southdown × B.L.-Cheviot has the highest muscle : bone ratio
followed by Cheviot and Iceland, while the Uruguay and Suffolk and
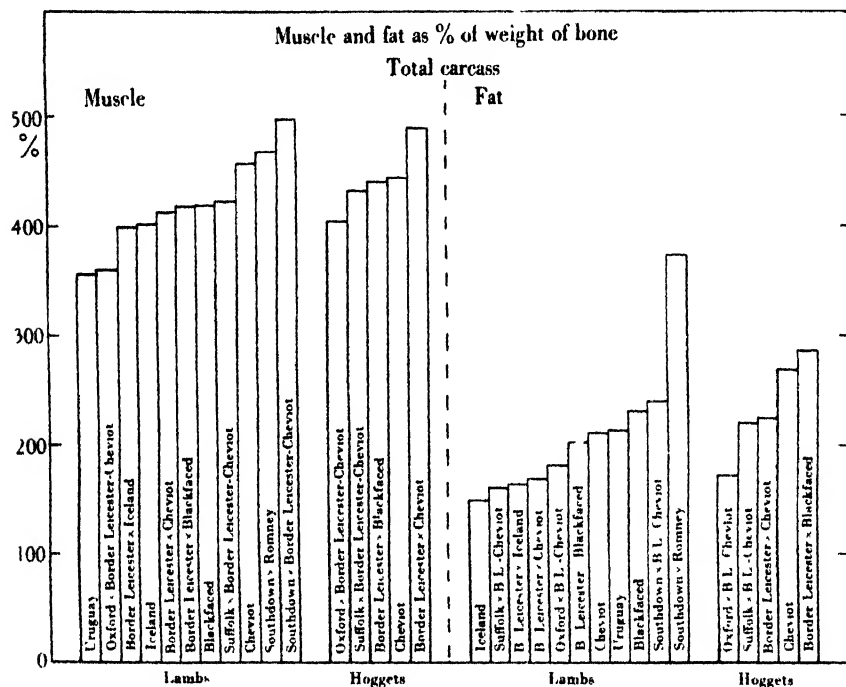
Text-fig. 17.

Oxford crosses with the B.L.-Cheviot have relatively least muscle as a
percentage of the bone weight. The muscle in the latter is less than three
times the weight of the bones but in the former about 4·5 times. In the
hoggets the B.L. × Cheviot has the highest muscle : bone ratio and is
comparable with the Southdown × B.L.-Cheviot lamb. The Suffolk ×
B.L.-Cheviot and Cheviot have the least muscle relative to bone.

Loin. In the loin the Southdown crosses are of outstanding merit
(see Text-fig. 16). They have nine times more muscle than bone. The
muscle in the loin of the Uruguay is only five times the weight of bone.
The Oxford × B.L.-Cheviot and B.L. × Iceland are slightly better, having
about six times more muscle than bone in the loin. The hoggets differ

greatly in muscle : bone ratio in this joint. The B.L. × Cheviot is the best, having nine times more muscle than bone, and the Oxford and Suffolk crosses with the B.L. × Cheviot the poorest, the former having only 6·6 times more muscle than bone in the loin.

Total carcass. The order of merit of the different breeds in respect of their muscle : bone ratio is best judged from the proportions in the total carcass in conjunction with that of the loin. The Southdown × B.L.-Cheviot is the best, followed by the Southdown × Romney, Cheviot and Suffolk × B.L.-Cheviot. The B.L. × Blackfaced, Blackfaced and Iceland are considerably inferior. The poorest is the Uruguay and Oxford × B.L.-Cheviot. The order of merit in respect of carcass quality is also dependent on the relative amount of fat in each joint and the influence of this character on the order of merit will be referred to in subsequent sections. The descending order of merit in the hoggets is: B.L. × Cheviot, B.L. × Blackfaced, Cheviot, Suffolk × B.L.-Cheviot and Oxford × B.L.-Cheviot. Thus at both ages the Oxford × B.L.-Cheviot appears to have least muscle relative to bone of all the Scottish breeds and crosses.

(b) Proportions of muscle in different joints as a percentage of the weight of muscle in the neck.

Table 75 shows the breed differences in proportions of muscle in different regions of the body relative to the amount of muscle in the neck. The Southdown × B.L.-Cheviot is outstandingly superior to the other breeds in this respect. Its muscle in the loin relative to that of the neck is nearly twice as heavy as in the Iceland and B.L. × Cheviot. It has proportionately more muscle in every joint relative to the muscle in the neck but the difference is less in the thorax than in other joints. The Iceland, Southdown × Romney, Uruguay and B.L. × Cheviot have relatively small amounts of muscle in all joints compared with that of the neck, but particularly is this so in respect of the late-maturing parts (loin and pelvis). Actually the proportion of muscle in the loin in the Southdown × Romney is fairly high considering that it has only five lumbar vertebrae. The lambs with seven lumbar vertebrae have all a high proportion of muscle in the loin relative to the neck, but this is apparently due more to the extra vertebrae than actual breed characteristics. The Blackfaced and the Suffolk cross have relatively little muscle in the pelvis compared with other joints, but this may be partly due to these having only four sacral vertebrae. In the hoggets the B.L. crosses have relatively the best developed muscles in the valuable cuts, followed by the Suffolk × B.L.-Cheviot and Cheviot. The Oxford × B.L.-Cheviot is the poorest in

this respect. The order of merit in the lambs and the hoggets is much the same except the B.L. × Cheviot hogget is relatively better than the lamb, which is probably due to its being above the average for that breed. The Oxford cross lamb had a relatively light neck probably due to individuality.

Table 75. *Proportions of muscle in each joint expressed as percentage of the weight of muscle in the neck*

Breed	No.	Wt. of muscle in neck g.	Head	Shoulders	Thorax	Loin	Pelvis	Legs
			Hoggets					
B.L. × Blackfaced	I	950	36	318	275	158	146	344
B.L. × Chev	II	1154	35	307	275	161	132	320
Cheviot	III	1119	33	280	254	142	117	313
Oxford × B.L.-Chev.	IV	1230	30	269	230	127	119	304
Suffolk × B.L.-Chev.	V	1177	28	311	260	152	125	354
			Lambs					
B.L. × Blackfaced	XI	675	47	279	312	159	121	396
B.L. × Chev.	X	888	36	223	251	119	92	310
Cheviot	XII	745	40	271	281	138	124	338
Oxford × B.L.-Chev.	VIII	716	49	285	261	162	120	356
Suffolk × B.L.-Chev.	VII	886	39	246	251	173	112	321
Southdown × B.L.-Chev.	VI	607	59	343	332	209	158	420
Blackfaced	IX	647	48	284	278	166	107	369
Uruguay	XIII	646	—-	264	265	127	104	369
Southdown × Romney	XIV	748	–-	237	247	133	82	313
B.L. × Iceland	XV	750	41	270	274	169	115	346
Iceland	XVI	962	43	199	216	115	105	264

(2) *Muscle measurements*

(a) *Measurements A, B, X and Shape Index of eye muscle.*

Table 77 shows the breed differences and age changes in the various muscle measurements. By comparison of these measurements with the average measurements for each breed at comparable weight (Appendix VI) one can obtain an idea of how far these representatives differ from the average for their breed. The B.L. × Cheviot hogget has exceptionally deep eye muscle compared with the average for that breed. The Suffolk × B.L.-Cheviot has the largest muscle measurements at both ages $(A+B+X)$. Depth of eye muscle is greatest in the lambs in the short-boned breeds, i.e. the Southdown crosses, Cheviot and B.L. × Blackfaced. It is doubtful whether the very long and shallow eye muscle of the Cheviot hogget is a characteristic of the breed. It rather appears to be due to individuality (see average measurements for Cheviot hoggets at different weights, Appendix VI). On the other hand the Cheviot lamb with the very short but deep eye muscle may be above that typical for the breed as this is the only Cheviot lamb which was studied. The Shape Index in

Table 76. *Fat measurements in lambs and hoggets of different breeds*

Measurements	B.L.× Black-faced		B.L.× Chev.		Cheviot		Oxford× B.L.-Chev.		Suffolk× B.L.× Chev.		Southdown× B.L.× Chev.	Black faced	Uruguay	Southdown× Romney	B.L.× Iceland	Iceland
No.	XI	I	X	II	XII	III	XIII	IV	VII	V	VI	IX	XIII	XIV	XV	XVI
Approx. age (months)	13	13	13	13	13	13	13	13	13	13	4·5	4·5	4·5	4·5	4·5	4·5
C	4·5	4·5	4·5	4·5	4·5	6·5	4·5	4·5	4·5	5	5	2·5	4	5·5	4	2
D	4	7	3	3·5	3·5	4	3	3	3·5	3	6	2	3	8·5	1	1
J	2	9	4	4	3	4	3	4	8·5	4	14	7·5	9·5	16·5	9	7
Y	10·5	15	8	13·5	10	14	10·5	8	16·5	9·5	5	3	3·5	6	3·5	2·5

Table 77. *Muscle measurements in lambs and hoggets of different breeds*

Measurements	B.L.× Black-faced		B.L.× Chev.		Cheviot		Oxford× B.L.-Chev.		Suffolk× B.L.× Chev.		Southdown× B.L.× Chev.	Black faced	Uruguay	Southdown× Romney	B.L.× Iceland	Iceland
No.	XI	I	X	II	XII	III	XIII	IV	VII	V	VI	IX	XIII	XIV	XV	XVI
Approx. age (months)	13	13	13	13	13	13	13	13	13	13	4·5	4·5	4·5	4·5	4·5	4·5
Length of eye muscle (A) mm.	57	57	59	61	55·5	65	55·5	60·5	63	64	55·5	58	56	51	58	56
Depth of eye muscle (B) mm.	29·5	31	26	35·5	30	27	24·5	27	28·5	34·5	29·5	25·5	23	27	28·5	24·5
Shape Index $\dfrac{B \times 100}{A}$	52	54	44	58	54	42	44	45	45	54	53	44	41	52	49	44
Thickness of muscle on rib (X)	12	13	11	15	12·5	11	11	14·5	13	14	13	12	10	18·5	12·5	10
Colour on beef scale	11	10	8	9	10	9	9	9	11	8	10	10	12	9	11	11

the lambs is best in the Southdown crosses, the Cheviot and B.L. ×
Blackfaced, but poorest in the Uruguay, Oxford × B.L.-Cheviot, B.L. ×
Cheviot and Iceland. This order of merit is much the same as given in
Part II. The Blackfaced lamb has poorer Shape Index than the average
for its weight class. The breeds do not differ very much in thickness of
muscle on the ribs. All the short-boned breeds and the Suffolk × B.L.-
Cheviot are the best in this respect. The muscle measurements are
numerically larger in the hoggets than in the lambs, and "B" increases
more than "A" with age as the Shape Index increases. This agrees with
Hirzel's results (1936). Pl. VIII illustrates the muscle and fat develop-
ment as seen at the last rib in lambs and hoggets. All the carcasses have
been photographed to the same eye muscle length (A constant) to show
up the relative difference in depth of eye muscle, which is the most
important measure of the two.

(b) *Colour of the eye muscle (Longissimus dorsi).*

Colour of muscle is of importance as a factor affecting the flavour of
the meat (Hammond, 1932, who reviews also an extensive literature
dealing with variation in the muscle colour of different muscles in the
same species). Recent work (Needham, 1926; Millikan, 1936) has estab-
lished the fact that colour of muscle is due to muscle haemoglobin which
differs from blood haemoglobin in characteristic properties. It has a
fatigue-resisting function, storing oxygen, this increasing with age and
exercise. Hammond (1932), in the sheep, has recorded the latter effects,
as also has McMeekan (1938) in the pig. That the diet is also capable of
affecting it is clear from the work of the latter, and from the fact
that the use of iron-containing foods must be avoided in veal production
if a pale colour is to be secured. The colour of the *Longissimus dorsi*
muscle at the last rib has been recorded by us in the lambs and hoggets
used in the dissection, as well as in some of the lambs which were
described in Part II. The colour was recorded on a colour chart specially
made for use on beef, but the latter differs in shade from mutton and
lamb. This beef scale was divided into 12 distinct shades, the palest (for
very pale veal) being 1 and the darkest (for dark bull beef) being 12.

Table 78. *Colour of eye muscles in lambs of different breeds*

Breed ...	Iceland	B.L. × Iceland	Black-faced	B.L. × Black-faced	B.L.× Chev.	South-down × B.L.-Chev.	Oxford × B.L.-Chev.	Suffolk B.L.-Chev.
No. of indi-viduals	47	40	9	10	13	11	20	8
Colour	10·75	10·95	10·8	10·3	10·38	9·0	8·95	10·25

Table 78 shows the effect of breed on the colour of the eye muscle in lambs. In the Iceland and B.L. × Iceland, data on lambs of both sexes as well as castrated males are lumped as there was no significant difference which could be attributed to sex. This fact must be attributed to the young age of the animals and that sex differences have not yet expressed themselves, rather than there being no difference in colour of muscle due to sex. Several workers have found sex to be a factor. Hall (1910) and Leighton & Douglas (1910) agree that the flesh of steers is lighter in colour than that of bulls. The range in colour (see Table 78) is from relatively light in the Oxford × B.L.-Cheviot to dark in the Iceland, Blackfaced and B.L. × Iceland. This supports the theory that exercise is an important factor affecting colour of muscle. The Oxford and Southdown crosses were very docile as compared with the Suffolk crosses, Blackface and Border Leicester crosses when handled before slaughter. The Iceland and B.L. × Iceland are both agile in nature and have to roam with their mothers over vast unenclosed mountain grazings in search of food. That exercise just prior to slaughter causes the muscles to become darker is evident from the data on the Iceland and B.L. × Iceland lambs. It is customary in Iceland to drive the animals on the hoof from the mountains in autumn and from the farms to the abattoirs where they are killed very shortly after arrival. The distance covered by some of the lambs may exceed 100 miles. The distance from the farm to the slaughter-house, to which most of the lambs used in this study were driven, varied from 5 to 30 miles. Those driven the shortest distance were killed immediately on arrival. In addition they had been gathered from the mountains very shortly before killing. 64 such lambs had the average colour of eye muscle 11·2. Some were darker than any shade on our chart and were classed as having colour shade 13. Another batch of 25 lambs was taken from a distant farm on a lorry and killed on arrival. These had an average eye-muscle colour of 9·9 only. Not one in this group was darker than 11. This is a very considerable difference as the maximum individual variation in muscle colour we have met in lambs is from 8 to 12 under normal conditions.

Table 77 shows that the colour of muscles in the hoggets is lighter than in the lambs of the same breeds. This is contrary to what could be expected, as Hammond (1932) in the sheep, and McMeekan (1938) in the pig have shown that colour of muscles increases with age. This condition may be due to two main causes. The food consumed by the hoggets in winter (turnips and concentrates) may be relatively deficient in iron-containing substances as compared with the food (green succulent grass)

received by the lambs in summer. The other factor and most likely the more important one is the fact that the lambs have more exercise following their mothers and playing about in fields and pastures as compared with the hoggets which are usually folded closely on roots.

(c) The size of muscle bundles (grain) of the Longissimus dorsi.

Hammond (1932) states that the size of the muscle bundles has probably much to do with the texture and eating qualities of meat. He quotes Diffloth (1908), who says that the finer the grain the better the meat. A muscle with a fine texture is believed to be more palatable than a coarse one, which is often stringy when cooked. A great variation in coarseness of grain in different muscles of the same animal has been met with (Hammond, 1932). He also found that the size of muscle bundles became greater with age and that breeds differ in coarseness of grain. As the number of muscle fibres (muscle cells) does not increase after birth the thickness in the muscle bundles with age is due to increase in size of the muscle fibres.

It is exceedingly difficult to measure the average size of muscle bundles as seen in cross section as these vary considerably in the same muscle both in size and shape. We have therefore adopted the same method as Hammond (1932) to judge breed differences in size of muscle bundles by eye. A section cut across the grain of the central part of the *Longissimus dorsi* over the last rib, stained in Van Gieson's stain and mounted in Canada balsam, was used for this purpose. Photographs of a slide from each sheep were obtained as a direct print by placing the slides in a photographic enlarger and printing to the same linear scale (×5). These are given in Pl. IX, Nos. I–XVI referring to the sheep in question, the corresponding age and breed of which are given in Table 79. The difference in size of grain was judged independently by four different persons, all of whom were well acquainted with histological work. The labels were covered during judgement to avoid possible prejudice. A range of 20 points was allowed for, the coarsest grain giving 10 points and the finest 30 points. The average of these points from the four judges are given for each breed in Table 79. The breed differences are marked. The Iceland and the Blackfaced have the smallest muscle bundles. The Cheviot has larger grain than the Blackfaced. The effect of this is clear from a comparison of the B.L. × Blackfaced and B.L. × Cheviot. At both ages the latter has decidedly coarser grain. All the Border Leicester crosses have larger grain than the mother breeds (Blackfaced, Iceland and Cheviot), indicating that the Border Leicester has very large grain. The Suffolk and

Oxford crosses do not differ greatly, but have smaller muscle bundles than the B.L. × Cheviot. The Southdown × B.L.-Cheviot is coarse-grained. The Uruguay has, however, the largest muscle bundles.

Table 79. *Breed differences in the size of muscle bundles (grain)*
in the Longissimus dorsi

10 = largest.　　　30 = smallest bundles.

Breed ...	B.L. × Blackfaced		B.L. × Chev.		Cheviot		Oxford × B.L.-Chev.		Suffolk × B.L.-Chev.	
Age (mo.)	4·5	13	4·5	13	4·5	13	4·5	13	4·5	13
No.	XI	1	X	II	XII	III	VIII	IV	VII	V
Size of bundles	21	25	13	18	21	24	22	23	25	20

Breed ...	Southdown × B.L.-Chev.	Blackfaced	Uruguay	Southdown × Romney	B.L. × Iceland	Iceland
Age (mo.)	4·5	4·5	4·5	4·5	4·5	4·5
No.	VI	IX	XIII	XIV	XV	XVI
Size of bundles	12	29	10	20	23	30

C. FAT DEVELOPMENT

(1) *Relative weight of fat in different joints*

(a) Weight of fat in each joint as a percentage of the weight of bone.

Table 74 and Text-figs. 11–17 show the amount of fat in each joint and in the total carcass as a percentage of the weight of bone. These diagrams illustrate also the relative amounts of fat to muscle as both are shown as a percentage of the same weight (bone). As in muscle, there are relatively less breed differences in the fat : bone ratio in the thorax and neck than in the whole carcass, and the greatest in the loin and pelvis. In each joint and the total carcass the Southdown × Romney is proportionately fatter than any other lamb. It is also fatter than any of the hoggets. For lamb, it can be considered excessively fat in all the joints except legs and shoulders: In the thorax it has more fat than muscle and practically as much fat as muscle in the neck, loin and pelvis. This cannot be regarded as a fault in the breed but rather due to faulty marketing in not killing it at a lighter weight. In this connexion it must be remembered that this lamb is not typical of the commercial New Zealand lamb as regards management. Killed late in the season it is more typical of the lambs which, bred on hill country, are reared on a plane of nutrition inadequate to permit slaughter at/or before weaning time as is characteristic of the higher quality New Zealand product. It is subsequently

fattened on good pastures on the lowlands. This is likely to retard the muscular development relative to fat, as compared with lambs marketed early in the season which are killed straight from their mothers at from 3 to 4 months old. The Southdown × B.L.-Cheviot comes next in proportional state of fatness. It can be considered to have very desirable proportions of fat to muscle. It is significant that this lamb is the second fattest lamb in all the most valuable joints, some of which are inclined to be too lean in early life and in late-developing breeds (legs, loin, shoulders), but is below average in the neck and but slightly above the average in the thorax, both of which tend to be too fat and are cheap cuts (see Text-figs. 11–17). This is a characteristic showing both the early developing tendency of this cross as well as the desirable meat quality of an animal of this form. It will be noticed that the order of increasing fat: bone ratio differs considerably from the order of increasing muscle : bone ratio. Generally (see Text-figs. 11–17) the smaller breeds show more fat relative to bone than the larger breeds with two important exceptions. The Uruguay lamb, which had the lowest muscle : bone ratio of all the lambs, approaches the Southdown × B.L.-Cheviot in the fat : bone ratio. The Oxford × B.L.-Cheviot lamb is comparable in this respect though not quite so fat as the Uruguay. This makes the muscle : fat ratio much lower in these lambs and thus indicates relatively poor quality Their state of fatness, however, makes them marketable at relatively light weights. This condition shows the great necessity of taking various other factors, such as conformation and muscular development, into account besides the ' finish " (state of fatness) of the carcass when judging meat.

The Iceland, Suffolk × B.L.-Cheviot, B.L. × Cheviot and B.L. × Iceland have the lowest fat : bone ratio in the total carcass, and in the individual joints, but their order varies slightly in the different joints. This indicates the relatively low rate of fat metabolism in these breeds in early life, which is a sign of late maturity. Lambs of these breeds cannot be considered of very good quality at this weight. Their very low fat : muscle ratio in the limbs is objectionable. There is no available evidence to show that these breeds do not yield carcasses of satisfactory quality at heavier weights. On the contrary, animals with body conformation and proportional development of muscle as the Suffolk cross and B.L. × Iceland should yield good quality carcasses at heavy weights. This has been found to be the case with the former (see Part II). The hoggets are relatively fatter than the lambs of the same breeds. The B.L. × Blackfaced is relatively fattest in all the joints but the neck, where Cheviot has the highest fat : bone ratio. The former can be

considered overfat, particularly in the pelvis and loin. This indicates the early development of this cross which has been referred to several times above. The Oxford × B.L.-Cheviot is relatively leanest in all the joints but the neck and can be considered too lean, particularly in the loin and legs. As it has also the lowest muscle : bone ratio in the total carcass and all the joints but the neck and pelvis it must be considered of the poorest carcass quality of the hoggets from the point of view of composition. From Text-figs. 11–17 it is obvious that the proportion of fat to muscle varies much in different joints. The pelvis is relatively fattest, followed by the thorax and neck, all which are fatter than the average for the total carcass. The legs are relatively leanest, having less fat than bone in some breeds. The shoulders come next, followed by the loin.

(b) *Proportions of fat in different joints relative to the weight of fat in the neck.*

The distribution of fat in the different joints of the carcass relative to the fat in the neck is shown in Table 80. As the neck is a cheap joint and also inclined to contain high proportions of fat to muscle it is desirable that the fat in the more valuable parts (loin, legs) should be relatively well developed. On the other hand the kidney fat, which is of little value to the butcher, should be relatively light. The Iceland and Blackfaced have proportionately the heaviest kidney fat. The Southdown × B.L.-Cheviot has also proportionately heavy kidney fat, but this is more due to the very little fat in the neck of this breed rather than actually heavy kidney fat. The Uruguay, Suffolk × B.L.-Cheviot and Southdown × Romney have a relatively small amount of kidney fat. In other joints the relative amount of fat varies in different order. The Iceland has proportionately very little fat in loin and legs as compared with the Southdown crosses and the Oxford × B.L.-Cheviot, which have less kidney fat. This shows the greater tendency in the mountain breeds to accumulate more internal fat and less subcutaneous fat on the loin and leg than the more specialized meat breeds (Southdown, Suffolk and B.L. crosses). In the carcass classes at Smithfield, Hammond (1921) found that the percentage of the caul and gut fat in wethers of 21 months old varies from 8·23 % in the Blackfaced Mountain to 5·68 % in the Southdown, while the measurements of the subcutaneous fat at the last rib (see Hirzel, 1936) is greater in the Southdown. Hammond (1932) quotes Ewart (1878) who states that breeds which have an aptitude for becoming fat at an early age deposit larger quantities of external fat than do late-maturing breeds. He also states that great fatness in the parts of the body with a moderate

quantity on the upper part is an indication of a large yield of fat in the kidney and caul, which agrees with our results. The Iceland and Blackfaced lambs have a relatively thin layer of fat cover on the loin (C) (see Pl. VIII) relative to the weight of fat in the body and the Iceland breed is noted for its marked tendency to fatten on the sternum and yield a high percentage of internal fat. There is undoubtedly some definite physiological reason for the tendency to accumulate fat differentially in different regions. It will be noticed that those breeds which fatten most round the internal organs have to forage for themselves and often subsist on a very low plane of nutrition during winter, while those which deposit more fat on the carcass are most dependent on artificial feeding. Therefore it is not an unlikely explanation that fat round the internal organs is a readier store of energy for the animal for maintenance when on a submaintenance level of nutrition than is fat deposited on the carcass. A knowledge of the regions of the body first to lose fat when a fat animal is on a submaintenance level of nutrition would give valuable information on this point.

Table 80. *Proportions of fat in different joints expressed as percentage of weight of fat in the neck*

Breed	No.	Wt. of fat in neck g.	Head	Shoul-ders	Thorax	Loin	Pelvis	Legs	Kidney fat
			Hoggets						
B.L. × Blackfaced	I	599	41	264	421	205	222	168	140
B.L. × Chev.	II	484	45	278	429	188	227	185	117
Cheviot	III	745	22	202	333	154	165	146	146
Oxford × B.L.-Chev.	IV	674	24	179	286	85	131	127	83
Suffolk × B.L.-Chev.	V	650	30	230	376	181	166	148	101
			Lambs						
B.L. × Blackfaced	XI	500	14	123	286	123	134	134	100
B.L. × Chev.	X	525	15	109	236	98	108	112	78
Cheviot	XII	448	18	166	307	125	130	130	139
Oxford × B.L.-Chev.	VIII	448	23	194	324	140	141	142	95
Suffolk × B.L.-Chev.	VII	462	22	142	275	133	127	113	69
Southdown × B.L. Chev.	VI	350	19	254	384	178	202	191	131
Blackfaced	IX	538	17	146	260	131	105	124	117
Uruguay	XIII	578	—	115	281	107	125	96	50
Southdown × Romney	XIV	790	—	140	267	112	97	128	71
B.L. × Iceland	XV	399	47	158	317	147	141	128	99
Iceland	XVI	445	18	104	258	111	139	93	176

In the hoggets the B.L. crosses have the most desirable proportions of fat in the various joints, having relatively large amounts in the legs, loin and pelvis. The Oxford × B.L.-Cheviot has proportionately very little fat in the loin and the legs. This is partly due to the relatively heavy

neck of this sheep, but also due to the absolutely low percentage weight of
fat in the valuable parts of the body (see Table 88). The Cheviot has large
fat deposits accumulated in the neck and round the kidneys at this age,
but due to its generally fat condition it is not deficient in fat in the loin,
pelvis and legs. It will be noticed that the Cheviot hogget is of relatively
poorer quality than the Cheviot lamb, mainly due to inferior body
proportions. Two differences in the skeleton were marked, the hogget
having long, badly sprung ribs and heavy neck vertebrae as compared
with the lamb. Whether the differences in carcass quality (poorer
muscular development and body proportions of the hogget) can be
attributed to these differences in conformation is not certain.

(2) *Fat measurements*

(*a*) *Linear measurements.*

Table 76 shows the breed differences in the fat measurements taken
at the last rib (see Parts I and II). This is further illustrated in Pl. VIII.
Measurement "*C*" which is the most important of these is deficient in all
the lambs except the Southdown crosses, B.L. × Blackfaced, B.L. ×
Iceland and the Uruguay. As referred to above it is most deficient in the
Iceland and the Blackfaced. In the latter this is surprising as the carcass
as a whole and even the loin contains relatively large amounts of fat
(see Table 88 and Appendix III). But, as referred to above, these breeds
tend to lack subcutaneous fat on the back relative to the amount of fat
in other parts of the body. In the hoggets the B.L. × Blackfaced and
Cheviot have the ideal "*C*" measurement and the Suffolk × B.L.-Cheviot
is good in this respect. The B.L. × Cheviot and Oxford × B.L.-Cheviot are
too lean on the loin. The latter however has a carcass of very good
quality, but would have been nearer the ideal at slightly heavier weight,
which would have been followed by more subcutaneous back fat. The
"*D*" measurement varies greatly with breed, but is not a direct measure
of the state of fatness of the carcass (Parts I and II). The Southdown
crosses have thick fat at "*D*" as well as very short spinous process (see
Nos. XIV and VI, Pl. VIII). This latter character is of importance in
making the cutlet more attractive. The Iceland and B.L. × Iceland have
a very thin layer of fat at "*D*" with very high spinous process (see
Nos. XV and XVI in Pl. VIII and Appendix II). The sharpness of the
"withers"—which is either due to high spinous process, poor develop-
ment of the *Longissimus dorsi* or badly sprung ribs, individually or
collectively, as compared with flat broad, oval "withers", is illustrated in
Pl. VIII. The Iceland and to a less extent the Uruguay, B.L. × Cheviot

and Oxford × B.L.-Cheviot have sharp "withers", and the Southdown crosses, the Cheviot, B.L. × Blackfaced and Suffolk × B.L.-Cheviot, broad ones. The latter have decidedly more attractive appearance from the quality point of view. The Southdown × Romney has an excessive thickness of fat at "*J*" and would require trimming to make the cutlets of prime quality. The same can be said of the Suffolk × B.L.-Cheviot and B.L. × Blackfaced hoggets. None of the breeds are deficient in "*J*" measurement because the fat requirement is very low at this point for the underlying muscle layers are very thin. There are but small and unimportant breed differences in measurement " *Y* ". The Suffolk × B.L.-Cheviot and B.L. × Blackfaced are slightly too fat at this point. All the fat measurements are larger in the hoggets than the lambs except in the Oxford × B.L.-Cheviot. The hoggets have relatively greater "*J*" and " *Y* " than " *C* " and " *D* ". This shows a tendency for overfattening on the ribs with age, which often makes it necessary for the butcher to trim fat carcasses before they are retailed.

(b) Intramuscular or "marbling" fat.

The fat deposited within the muscles, chiefly in the connective tissue between the muscle bundles and round the blood vessels (marbling fat), has been weighed with the muscles, thus increasing the weight of muscle relatively more in those animals having much marbling fat. Hammond (1937 *b*) states that marbling fat is not of much importance in mutton, which is already relatively tender but is of importance in beef for it improves the cooking qualities and tenderness of the muscle. The amount of marbling fat varies slightly in different muscles of the body (Hammond, 1932). We have compared the breeds in respect of marbling fat contained in the *Longissimus dorsi* muscle at the last rib. A sample of that muscle was retained for chemical and histological work and fixed in 10% formalin. We have not yet made a chemical study of the amount of marbling fat contained in this muscle in different breeds. Hammond (1932) found that an histological test for marbling fat agreed fairly well with a chemical test. We have therefore only studied the marbling fat histologically. Transverse sections were cut from the same part of the muscle (the central part of the *Longissimus dorsi* over the last rib) from each animal, stained with Sudan III and examined by placing in a lantern and projecting them on a screen. Pl. X*a, b* shows photographs of the most typical sections for each breed, enlarged (× 3·5). Of the lambs the Southdown × Romney is most marbled, followed by the Cheviot, Blackface, Uruguay and Oxford × B.L.-Cheviot. The B.L. crosses come next in

order, followed closely by the Southdown × B.L.-Cheviot and Iceland, while the Suffolk × B.L.-Cheviot has practically no marbling fat. The hoggets have slightly more intramuscular fat (marbling fat) than the lambs of the same breeds, particularly in the case of the Suffolk cross. The Cheviot is most marbled followed by the B.L. × Blackfaced, B.L. × Cheviot, Oxford × B.L.-Cheviot and Suffolk cross B.L.-Cheviot. This shows that, in general, the fattest animals have most marbling fat though exceptions do occur, such as the Southdown × B.L.-Cheviot lamb having less marbling fat than several other lambs relatively leaner. Similarly the Suffolk cross hogget, a fatter animal than the Oxford cross, has less intramuscular fat than the latter. Hirzel (1936) noted that marbling fat increases with the state of fatness of the animal.

§ II. AGE CHANGES IN RELATIVE DEVELOPMENT OF BONE, MUSCLE AND FAT

A. SKELETAL DEVELOPMENT

(1) *Comparative development of bones in different joints*

Table 81 gives the weight of bone in each joint in the hoggets expressed as a percentage of the weight of bone in the same joints in lambs of the same breed. This shows the relative difference in bone development in the various regions of the body with increase in age from 4·5 to 13 months and increase in carcass weight from 40 to 60 lb. It must be realized that these changes cannot be taken as directly due to age and weight as the hoggets have been reared on a lower plane of nutrition in early life than the lambs. The hoggets are likely to be physiologically younger in their development than their age would indicate. This study however serves the useful purpose of demonstrating the relative state of development in animals which have been kept for a prolonged time on a low plane of nutrition compared with animals of the same breed kept for a relatively short time on a higher plane of nutrition. It is striking that in the hoggets the bones of the forequarters, head, neck, shoulders and thorax, are relatively much better developed than in the hindquarters and feet. The bones in the forequarters are in all joints proportionately heavier than the average for the total skeleton and in the hindquarters the opposite is the case. The ratio in thorax is upset by the irregularity in the number of thoracic vertebrae and ribs. It is relatively too low in the B.L. crosses as the lambs of these breeds had 14 thoracic vertebrae. On the other hand the ratio is too high in the Cheviot and Suffolk cross owing to there being 14 thoracic vertebrae in the hoggets of these breeds. Hammond

Table 81. *Proportional weight changes in the skeleton with age*

Weight of bone in hoggets expressed as percentage of the weight of bone in lambs of the same breeds.

Joint	Breed ... No. ... Age (mo.) ...	B.L. × Blackfaced I 13	B.L. × Cheviot II 13	Cheviot III 13	Oxford × B.L.-Chev. IV 13	Suffolk × B.L.-Chev. V 13
Head		137	133	141	146	170
Neck		141	146	147	151	156
Thorax		135	125	155	148	158
Shoulders		136	133	150	143	148
Loin		111	126	137	115	125
Pelvis		130	125	160	125	153
Legs		123	129	142	130	132
Feet (4)		121	125	141	121	138
All joints − head and feet		130	129	149	138	146
All joints + head and feet		131	130	147	137	149

(1932) found that the rates of bone growth occurring after birth in the different areas of the body were as follows. The greatest rate of growth occurs in the pelvis and lumbar vertebrae, followed by the ribs and sternum, cervical vertebrae and upper parts (above cannon) of the fore- and hind-limbs in the order named. The parts which constituted the trunk of the animal developed more in postnatal life than the extremities—the head and the lower parts of the limbs. The rate of growth of the thoracic vertebrae, though greater than that of the head in early life, falls below it later in life. Our hoggets at 13 months thus differ least from the lambs at 4·5 months in the latest-developing parts (loin) and the earliest-developing parts (feet). The difference is greatest in the regions of intermediate rate of development (shoulders, neck and thorax). McMeekan (1938) has shown that time and nutrition (shape of the growth curve) are the two factors of major importance in determining bone growth. Hammond (1932) suggested and McMeekan (1938) demonstrated that an early-developing part or tissue has a prior call on the available nutrients, and that in consequence under-nourished animals remain relatively less developed in the late-developing regions of the body. In our case also the age at which the bones in different regions have the capacity for rapid growth appears to affect the relative development. Thus the relative difference between lambs and hoggets is less in respect to early-developing bones (feet) than in late-developing units (all joints) (see Table 81). The relative difference in the lumbar vertebrae at first sight is at variance with the situation. On examination however it is clear that the small relative growth in this late-developing region is quite compatible with the hypothesis of McMeekan (1938) that the differential effect of nutrition upon the animal body is due to the differential rates of growth of the

different parts. In the lambs the high plane of nutrition will have encouraged most the late-developing lumbar region. In the undernourished hoggets this part will have been penalized relatively more during the low nutrition period. The period of high nutrition during fattening has however not been long enough for sufficient growth in the loin to occur to provide the normal order of effect, though it is apparent that marked recovery has been made. The tendency for maximum differences between the parts falling into an intermediate order in development supports this picture, as also does the precisely similar results obtained by McMeekan in changing pigs from an initial low to a final high plane of nutrition.

The general bone development appears to be largely functional. The feet in sheep develop early because they are required for carrying the body in following the mother in search of food. Hammond found that the head, particularly the cranium, is large at birth but develops slowly during suckling period, but after weaning it grows rapidly, particularly the facial parts and the lower jaw. The fact that the bones in the head are relatively very heavy in the hoggets as compared with the lambs. which are killed prior to or shortly after weaning, further confirms this. The relatively great increase in the neck vertebrae with age is suggested by Hammond to be due to its function of accommodating large important nerves. As the neck acts as a lever on which the weight of the head is balanced, it is likely that the growth of the neck vertebrae must closely follow the growth of the head bones not to upset the balance.

There are considerable breed differences in the proportional weight of bones in the hoggets as compared with the lambs. The Cheviot hogget has proportionately heavy bones as compared with the lamb. In the late-developing parts (pelvis, loin) it is better developed than in the other breeds. This may be due to its smaller size (shorter bones) for, at the same weight as the larger breeds, it has reached a more advanced state of development. The proportionately much lighter bones in the Border Leicester crosses than the other breeds may be due to, in the case of the B.L. × Blackfaced, its early-developing tendencies (combined with absolutely light bones), i.e. it has. as a lamb at 4·5 months. attained more of its ultimate bone growth than have other breeds. In the B.L. × Cheviot this may be due more to the hogget being a slightly shorter and lighter-boned individual than the average for the breed, as has been referred to above. From the butcher's point of view the differences in relative development of the fore- and hindquarters in hoggets as compared with lambs are important. Hoggets have a relatively poorer development of the hind and valuable cuts of the carcass.

Table 82. *Weight of bones of the hind-limbs expressed as percentage of the weight of the cannon (metatarsal)*

Average for both limbs used for calculation.

Breed	No.	Actual wt. of cannon g.	Pelvis	Femur	Patella	Tibia fibula	Calcaneus	Astragalus	Other tarsals
			Hoggets						
B.L. × Blackfaced	I	50·0	458	277	14	242	34	24	21
B.L. × Chev.	II	53·35	409	294	17	247	36	28	23
Cheviot	III	50·1	469	304	16	261	39	28	23
Oxford × B.L.-Chev.	IV	60·0	425	301	19	258	36	30	23
Suffolk × B.L.-Chev.	V	63·5	449	265	14	239	35	25	22
			Lambs						
B.L. × Blackfaced	XI	41·5	426	282	14	222	35	27	22
B.L. × Chev.	X	44·05	411	280	14	227	34	27	23
Cheviot	XII	35·6	424	317	15	239	38	31	25
Oxford × B.L.-Chev.	VIII	51·5	380	274	14	222	35	29	22
Suffolk × B.L.-Chev.	VII	45·4	393	299	15	230	36	30	23
Southdown × B.L.-Chev.	VI	36·0	400	296	17	235	35	30	25
Scotch Blackfaced	IX	38·0	384	272	16	232	32	26	24
B.L. × Iceland	XV	43·0	437	293	14	231	36	22	23
Iceland	XVI	48·0	412	290	16	241	35	25	21

(2) *Age changes in weight of the individual bones of the limbs*

Hind-limb.

The weight of the bones of the hind-limb above the cannon have been expressed as a percentage of the cannon bone weight in lambs and hoggets to show the relation between the growth of the bones in the upper part of the limb and that of the cannon with increase in age (see Table 80). Hammond (1932) found that there was a growth gradient up the limb; the cannon grew least in postnatal life of all the long bones. The tarsals which grow mainly in thickness increase less in weight than the cannon after birth though situated higher in the limb. The tibia increased in weight more than the cannon and the femur more than the tibia. Our data, due to the fact that the hoggets have been reared on different levels of nutrition from the lambs, are not directly comparable with Hammond's data in this connexion. We find that the tarsals are relative to the metatarsal of much the same weight at 4·5 and 13 months. The tibia has increased in all the breeds at a faster rate than the cannon, but the femur on the other hand is in three cases out of five proportionately heavier in the lamb. This is probably due to the fact that the femur, a relatively late-developing bone, has suffered more through lack of nutrition in the hogget than the tibia. In the lambs the former has had a chance to develop relatively more because of the relatively high plane of nutrition on which the lambs have been kept (see p. 42). The pelvis was found by

Table 83. *Weight of bone in the fore-limbs expressed as percentage of the weight of the cannon (metacarpal)*

Average of both limbs used for calculation.

Breed	No.	Actual wt. of cannon g.	Scapula	Humerus	Radius-ulna	Carpals
		Hoggets				
B.L. × Blackfaced	I	47·65	195	246	199	33
B.L. × Chev.	II	53·1	168	242	185	40
Cheviot	III	49·0	185	242	195	37
Oxford × B.L.-Chev.	IV	60·9	173	242	204	35
Suffolk × B.L.-Chev.	V	63·0	176	214	178	32
		Lambs				
B.L. × Blackfaced	XI	38·95	153	237	168	38
B.L. × Chev.	X	43·1	154	225	172	39
Cheviot	XII	36·0	151	232	179	35
Oxford × B.L.-Chev.	VIII	49·0	148	216	170	36
Suffolk × B.L.-Chev.	VII	42·5	145	241	184	39
Southdown × B.L.-Chev.	VI	34·5	155	230	165	38
Scotch Blackfaced	IX	37·8	155	216	171	33
B.L. × Iceland	XV	42·0	164	244	194	38
Iceland	XVI	45·0	157	227	180	33

Hammond to be later-developing than the femur. We find that it has increased at a faster rate relative to the cannon than the femur. In the fore-limb (Table 83) the position is very similar. The radius-ulna increases in weight with age more than the cannon and more than the humerus, particularly in the large breeds (Oxford and Suffolk crosses). The latter, however, are proportionately heavier in the hoggets of the Cheviot and the Border Leicester crosses. The scapula increases more with age than any of the other limb bones. It is striking that in the large breeds (Oxford and Suffolk crosses) the upper bones of the limbs are proportionately lighter than those of the small breeds (Cheviot) as compared with the cannon. This is contrary to Hammond's results as he found the upper bones of the limbs heavier in the large breeds (Lincoln, Suffolk) than in the small breeds (Southdown, Welsh). This difference in our results may be due to the fact that our lambs and hoggets are of constant carcass weight respectively. In the large breeds growth has been retarded relatively as compared with small breeds. This has consequently affected the late-developing parts and tissues more than the early-developing ones (see under muscle and fat later).

B. Muscle development

(1) *Comparative development of muscle in different joints*

The relative distribution of muscle in hoggets as compared with lambs is shown in Table 84. Weight of muscle in each joint in the hoggets is expressed as a percentage of the weight of muscle in the same joints in the lambs. The relative effect of age on the muscle surrounding the tibia in the hind-limb and radius-ulna in the fore-limb compared with those surrounding the upper bones of the limbs is shown by keeping the two sets of muscles separate. As compared with the muscle in the total carcass there is least increase in muscle of the head with age. The muscle in the legs and thorax increases less than in the carcass as a whole. The increase of muscle with age is greatest in the pelvis and shoulders, followed by the loin. The neck is in an intermediate position. The relatively poorer development of the muscles of the loin (the latest-developing joint) than of the shoulders can be explained in the same way as the similar condition in the skeleton. There is more increase in muscle with age in the large breeds (Suffolk and Oxford crosses) in the early-developing parts (legs) than in the smaller breeds, while the opposite is the case in the loin. This demonstrates the relatively greater effect of undernourishment on the large-framed breeds than the smaller-framed ones when the carcass

weight of both types is the same. Hammond (1932) showed that the thigh muscles were later-developing (grew more in postnatal life) than the leg muscles (surrounding the tibia-fibula). We find that the thigh muscles (surrounding the femur) in the hoggets are proportionately heavier than the leg muscles compared with the same muscles in the lambs. In one case (B.L. × Blackfaced) this is not the case. This may be due to individuality or cutting error in jointing. The difference in the smaller breeds is less than in the larger ones (Suffolk and Oxford crosses). In the fore-limb similar conditions exist. The shoulder muscles (surrounding the scapula and humerus) have increased more than the arm muscles (surrounding the radius-ulna) with increase in age. The difference between the two sets of muscles is greater in the fore-limbs than in the hind-limbs.

Table 84. *Proportional weight changes in muscle with age*

Weight of muscle in hoggets expressed as percentage of the weight of muscle in lambs of the same breeds.

Breed .	B.L. × Blackfaced	B.L. × Cheviot	Cheviot	Oxford × B.L.-Chev.	Suffolk × B.L.-Chev.
No. ...	I	II	III	IV	V
Joint Age (mo.)	13	13	13	13	13
Head	106	125	123	105	98
Neck	141	130	150	172	133
Thorax	124	142	135	152	137
Shoulder: Shoulder	165	185	158	169	172
Arm	130	140	134	136	146
Total	160	179	155	162	168
Loin	140	176	155	135	117
Pelvis	170	187	141	171	148
Legs: Thigh	120	134	141	148	150
Legs	136	131	129	136	134
Total	122	134	139	146	147
All joints + head	137	153	144	152	142

(2) *Development of muscle relative to bone*

Table 74 and Text-figs. 11–17 show relative changes in the proportions of muscle to bone with increase in age from 4·5 to 13 months. There is very little difference in the amount of muscle in the total carcass as a percentage of the weight of the skeleton (head and feet excluded) in lambs and hoggets. The hoggets have but slightly higher muscle : bone ratio. This indicates that muscle has been increasing at a comparable rate with bone with the age increase. Hammond (1932) in the sheep and McMeekan (1938) in the pig have found that muscle is later-developing than bone and grows proportionately more than the latter in the later stages of the development of the animal. Our results appear therefore to be caused rather by relatively low nutrition for a prolonged period in

early life, which retards the development of the later-developing tissues as compared with the early-developing ones (McMeekan, 1938), than by normal growth. The fat : bone ratio is higher in the hoggets than the lambs, indicating that relatively more of the weight increase with age consists of fat than muscle or bone. Fat, the latest-developing tissue in the body, has therefore developed relatively more than muscle, which is contrary to what one would expect in animals on a low plane of nutrition. The hoggets are usually well fed for a relatively short period prior to killing. During this period large nutritive supplies may be available for production. Most likely this food is utilized for growth of all the tissues of the body, but the greater part of it is converted into fat as the muscle and bone have relatively less capacity for active growth at this age, and consequently require relatively little of the available nutrients. McMeekan (1938) records this result experimentally. In the thorax the muscle as a percentage of the bone weight is less in the hoggets than in the lambs. In the neck and legs it is practically similar at both ages. In the shoulders, pelvis and particularly the loin the muscle : bone ratio is higher in the hoggets. This indicates the relatively greater development of muscle as compared with the bone in the later-developing joints. Muscle in these regions of the body appears to have benefited more from the relatively good feeding just before slaughter than the muscle in the early-developing parts. This could be expected as the tissues in the late-developing parts will have their age for maximum rate of growth later in life than those of the early-developing regions.

C. Fat development

(1) *Comparative development of fat in different joints*

Table 85 shows the proportional weight changes in fat with increase in age in different joints. There is least increase in the weight of fat in the neck, in all the breeds, except the Oxford × B.L.-Cheviot. The legs come second. The kidney fat has increased at a comparable rate with the fat in legs. The fat has increased most in the shoulders, followed by the pelvis and loin, the thorax being in an intermediate position. The Oxford × B.L.-Cheviot differs however from the other breeds. The fat in loin of this cross has increased less than in any other joint. This fact is exaggerated by the seven lumbar vertebrae and consequently relatively more fat in the loin of the lamb of this cross. The fat in the head has increased very much with age in the smaller breeds, but less so in the large breeds (Oxford and Suffolk crosses). The general order of increasing fat in the

Table 85. *Proportional weight changes in fat with age*

Weight of fat in hoggets expressed as percentage of the weight of fat in lambs of the same breeds.

Breed		B.L. × Black-faced	B.L. × Chev.	Cheviot	Oxford × B.L.- Chev.	Suffolk × B.L.- Chev.
No.	...	I	II	III	IV	V
Joint	Age (mo.) ...	13	13	13	13	13
Head, subcutaneous and intermuscular fat		349	281	201	159	189
Neck: Subcutaneous		146	124	240	191	235
Intermuscular		101	72	133	124	75
Total		120	92	166	150	141
Thorax: Subcutaneous		209	189	204	94	224
Intermuscular		153	147	141	108	168
Total		176	167	180	133	193
Shoulders. Subcutaneous		214	194	230	116	239
Intermuscular (shoulder)		317	278	177	159	219
Intermuscular (arm)		167	357	239	168	194
Total		257	235	203	139	229
Loin: Subcutaneous		193	170	256	85	265
Intermuscular		216	190	148	100	73
Total		200	177	205	91	192
Pelvis: Subcutaneous		196	205	240	135	217
Intermuscular		209	173	156	150	119
Total		199	194	211	140	185
Legs: Subcutaneous		135	129	182	109	177
Intermuscular (thigh)		206	203	183	187	224
Intermuscular (leg)		242	328	268	254	131
Total		150	152	187	135	184
All joints – head: Subcutaneous		184	172	220	113	225
Intermuscular		183	167	162	153	149
Total		184	170	191	131	190
Kidney fat		168	137	177	132	205
All joints + head and kidney fat: Total		184	170	189	132	191

different joints with age is much the same as in muscle, except that there is relatively much more increase in fat than muscle in the head. The great increase in weight of bone in the neck is not followed by comparable increase in muscle and fat. It therefore appears that the neck is an early-developing joint in respect of muscle and fat development, but the great increase in bone could be attributed to their function. Table 85 shows that in neck, thorax, pelvis and in some breeds in the loin, the subcutaneous fat increases more with age than the intermuscular fat. This difference is particularly great in the neck. In the shoulders, legs and loin (in some breeds) the intermuscular fat increases more than the subcutaneous fat with age and weight. In the lower part of the limbs this difference is greater than in the upper part, i.e. the fat between the muscles surrounding the radius-ulna and tibia-fibula increases more than the fat between

the thigh and shoulder muscles. The subcutaneous fat in the Cheviot has increased more than the intermuscular fat in all joints but the leg. This is probably partly due to the relatively fatter condition of this breed than the others as well as a breed characteristic. It can be considered a point in favour of the breed, as it is indeed a lack of subcutaneous fat which often makes carcasses unsaleable. In total fat the Suffolk × B.L.-Cheviot increases most, followed by the Cheviot and B.L. × Blackfaced. The Oxford × B.L.-Cheviot increases least. The relative increase with age in total fat is much greater than in bone or muscle except in the Oxford cross where muscle increases most. This latter may be due to individuality.

(2) Development of fat relative to bone

Table 74 and Text-figs. 11-17 illustrate the changes in fat relative to bone with age and weight increase. In all the joints but the neck fat has increased relatively more than bone. In the thorax this difference is very little. In the loin, fat has increased relatively much more than bone, but the relative difference is less in the pelvis, shoulders and legs. This demonstrates that the more valuable parts of the body benefit more from age and weight increase than do the cheaper cuts. It also shows the tendency for too much fat to be deposited in the loin region when the animal reaches a high degree of maturity (see Hammond, 1932).

§ III. VARIATION IN BODY PROPORTIONS AND THE PERCENTAGE COMPOSITION OF THE TOTAL CARCASS AND ITS MAJOR JOINTS

A. CONFORMATION AND BODY PROPORTIONS IN DIFFERENT BREEDS

Pl. XI shows the breed differences and age changes in body proportions in the various breeds under investigation. All the carcasses are photographed, suspended by means of a gamble of constant length, and scaled to the same leg length "F". This illustrates the relative compactness of the carcass and is a photographic measure to show the width of gigots relative to the leg length. The superior conformation of the Southdown crosses is outstanding. The Cheviot lamb also has very good conformation. The B.L. × Blackfaced, Blackfaced and Suffolk × B.L.-Cheviot are much alike in this respect and are in an intermediate position, followed by the B.L. × Iceland and B.L. × Cheviot. The Oxford × B.L.-Cheviot and the Iceland have very poor proportional development but the Uruguay is however poorest. The gigots of the latter as compared with the Southdown crosses give an excellent idea of the importance of short, thickly fleshed legs as compared with long, poorly fleshed narrow

ones. In the hoggets the breed differences in carcass conformation are not very great. The Oxford × B.L.-Cheviot is however relatively thinner fleshed than the other breeds.

The effects of rams of different breeds on the B.L. × Cheviot ewe are clear from Pl. XI. The Oxford has detrimental effect on the conformation, the Suffolk slightly improves it, while the Southdown has very great beneficial effects. The difference between an improved mountain breed (Cheviot and Blackfaced) as compared with an unimproved (Iceland) is very great. The effect of the Border Leicester rams on the Blackfaced and the Cheviot is also illustrated. The Blackfaced cross has relatively better conformation than the Cheviot cross (Halfbred). All these results agree with those described and discussed in Part II. The external carcass measurements are given in Appendix II. They will not be discussed further in this section as their relation to carcass composition and quality is dealt with in Part I. The proportional weights of different joints expressed as a percentage of the weight of the neck in the different breeds are given in Table 86. The value of the carcass to the butcher depends greatly on the relative weight of the different joints in the carcass as the price per pound in some joints (loin, legs) is much higher than in others (neck, thorax) (see following paragraph). In the lambs the South-down × B.L.-Cheviot is of outstanding merit in this respect. The loin of this cross weighs 178% of the neck whereas in the B.L. × Cheviot, Iceland and Uruguay it weighs only 103–107%. In the hoggets this joint weighs 104% of the neck in the Oxford × B.L.-Cheviot but 154% in the B.L. × Blackfaced. The lambs with seven lumbar vertebrae have proportionately heavier loins than other joints, which shows the value of increasing length in that region. In the pelvis the breed differences are similar to these, except the Southdown × Romney, Blackfaced and Suffolk × B.L.-Cheviot have a proportionately lighter pelvis than loin relative to the other breeds. The legs of the Southdown × B.L.-Cheviot are 328% of the neck weight and in the B.L. × Blackfaced 279%, but in the Southdown × Romney and Iceland only 220%. The breed differences in proportional weights of the legs in hoggets are not great, indicating the relatively better development of the extremities than the trunk of the Oxford × B.L.-Cheviot. The Southdown × Romney, Iceland, Uruguay and B.L. × Cheviot lambs have too heavy necks as compared with the other joints. The Southdown × B.L.-Cheviot, B.L. × Iceland, B.L. × Blackfaced and the Oxford × B.L.-Cheviot have much better proportions. In the hoggets the Oxford × B.L.-Cheviot has very heavy neck relative to the weight of other joints, the Cheviot comes second, while the Border Leicester crosses

Table 86. *Body proportion in lambs and hoggets of different breeds*

Weight of each joint expressed as percentage of the weight of the neck

Joint	Age	B.L. × Black-faced	B.L. × Chev.	Cheviot	Oxford × B.L.-Chev.	Suffolk × B.L.-Chev.	Southdown × B.L.-Chev.	Black-faced	Uruguay	Southdown × Romney	B.L. × Iceland	Iceland
Neck (actual wt., g.):	Lambs	1419	1699	1450	1439	1603	1145	1460	1530	1818	1472	1732
	Hoggets	1915	2003	2218	2344	2255	—	—	—	—	—	—
Thorax:	Lambs	296	248	231	276	258	340	261	256	256	276	233
	Hoggets	316	311	284	250	290	—	—	—	—	—	—
Shoulders:	Lambs	214	185	222	244	211	298	216	192	187	223	179
	Hoggets	280	284	242	233	267	—	—	—	—	—	—
Loin:	Lambs	130	103	117	138	146	178	136	107	112	144	105
	Hoggets	154	150	136	104	143	—	—	—	—	—	—
Pelvis:	Lambs	123	98	119	123	115	166	102	112	91	116	115
	Hoggets	162	150	132	116	132	—	—	—	—	—	—
Legs:	Lambs	279	236	254	273	253	328	249	237	219	258	222
	Hoggets	262	273	244	238	270	—	—	—	—	—	—
Kidneys + kidney fat:	Lambs	42	30	50	38	27	48	50	25	38	33	51
	Hoggets	50	35	51	30	35	—	—	—	—	—	—
Head:	Lambs	99	88	89	111	97	129	110	—	—	112	109
	Hoggets	106	101	88	88	102	—	—	—	—	—	—
Feet (4):	Lambs	50	44	44	62	50	57	49	—	—	54	45
	Hoggets	47	51	41	48	52	—	—	—	—	—	—

4-2

have the most desirable proportions. The changes in body proportions with age are illustrated in Table 87. The shoulders and pelvis show the greatest increase in weight with age, but the latter increases less in the Oxford and Suffolk crosses than the other breeds. The loin in the Cheviot and the Border Leicester crosses increases slightly less, but more so in the Oxford and Suffolk crosses. This condition is further exaggerated by the loin in the lambs of the two latter breeds having seven lumbar vertebrae, but even if an allowance for that is made their loin increase is less than in the smaller breeds with age. On the other hand the neck and legs in the larger breeds (Oxford and Suffolk crosses) increase more in weight with age than in the Border Leicester crosses. This illustrates the effect of limited nutrition in influencing more the later-developing parts of the body in those breeds which have genetic capacity to grow to a large size. The head increases less than the legs in the larger breeds but more in the smaller breeds. The kidneys and kidney fat increase much more in the Suffolk × B.L.-Cheviot, Cheviot and B.L. × Blackfaced than in the Oxford × B.L.-Cheviot and the B.L. × Cheviot.

Table 87. *Changes in body proportions with age*

Weight of different joints in hoggets expressed as percentage of the weight of the same joints in lambs.

Breed		B.L. × Blackfaced	B.L. × Cheviot	Cheviot	Oxford × B.L.-Chev.	Suffolk × B.L.-Chev.
No.	...	I	II	III	IV	V
Joint Age (mo.)	...	13	13	13	13	13
Head		145	136	151	129	147
Neck		135	118	153	163	141
Thorax		144	148	155	147	158
Shoulder		177	181	166	155	177
Loin		160	172	178	123	138
Pelvis		177	180	170	154	161
Legs		127	136	147	142	150
All joints – head		150	154	159	147	156
Kidneys and kidney fat		162	137	170	130	183
Total carcass + head		150	152	158	145	155

B. Percentage composition of the different joints and the total carcass

Table 88 shows the actual weight of each joint and the carcass (less head, feet and kidney fat) as well as their major constituents (muscle, fat and bone) expressed as a percentage of the total weight of each joint. As referred to above the percentage composition does not reveal whether there is actually large or small amounts of a particular tissue in a joint or whether this is only apparently the case because of a very small or large amount of another tissue. As an example the bone may constitute a

Table 88. *Proportions of muscle, fat and bone in different joints expressed as percentage of the weight of the joint*

Breed	No.	Neck						Thorax					
		Total wt. g.	Muscle	Subcutaneous fat	Fat intermuscular	Total fat	Bone	Total wt. g.	Muscle	Subcutaneous fat	Fat intermuscular	Total fat	Bone
Hoggets													
B.L. × Blackfaced	I	1915	49·6	15·8	15·5	31·3	14·1	6047	43·2	20·4	21·3	41·7	14·0
B.L. × Cheviot	II	2003	57·6	12·7	11·4	24·1	14·5	6230	50·9	18·2	15·1	33·3	13·9
Cheviot	III	2218	50·5	15·0	18·6	33·6	12·4	6310	44·8	18·5	20·8	39·3	14·1
Oxford × B.L.-Chev.	IV	2344	52·5	14·4	14·4	28·8	14·4	5860	48·4	10·9	22·0	32·9	16·8
Suffolk × B.L.-Chev.	V	2256	52·2	19·7	9·1	28·8	15·7	6550	46·7	18·9	18·4	37·3	15·5
Lambs													
Southdown × B.L.-Chev.	VI	1145	53·0	14·0	16·6	30·6	13·7	3889	51·8	17·2	17·3	34·5	13·9
Suffolk × B.L.-Chev.	VII	1603	55·3	11·8	17·0	28·8	14·1	4131	53·9	13·4	17·3	30·7	15·5
Oxford × B.L.-Chev.	VIII	1439	49·8	12·2	18·9	31·1	15·5	3976	47·0	17·1	19·4	36·5	16·7
Blackfaced	IX	1460	44·3	11·8	25·1	36·9	13·5	3810	47·2	14·1	22·7	36·8	14·8
B.L. × Chev.	X	1699	52·3	12·1	18·8	30·9	11·8	4213	52·9	14·2	15·2	29·4	16·4
B.L. × Blackfaced	XI	1419	47·6	14·6	20·6	35·2	13·7	4207	50·1	14·0	20·0	34·0	15·0
Cheviot	XII	1450	51·4	9·6	21·3	30·9	13·0	4075	51·5	14·0	19·8	33·8	14·1
Uruguay	XIII	1530	42·2	13·1	24·6	37·7	14·1	3920	43·6	18·5	23·0	41·5	14·9
Southdown × Romney	XIV	1818	41·1	16·2	27·2	43·4	10·6	4665	39·7	20·6	24·8	45·4	10·9
B.L. × Iceland	XV	1472	51·0	8·7	18·4	27·1	14·7	4067	50·6	13·3	17·8	31·1	15·7
Iceland	XVI	1732	55·5	7·3	18·4	25·7	12·9	4032	51·6	12·2	16·4	28·6	15·2

Table 88 (*continued*)

Breed	No.	Shoulders						Loin					
		Total wt. g.	Muscle	Subcutaneous fat	Fat intermuscular	Total fat	Bone	Total wt. g.	Muscle	Subcutaneous fat	Fat intermuscular	Total fat	Bone
Hoggets													
B.L. × Blackfaced	I	5369	56·2	13·3	16·2	29·5	11·9	2955	50·9	27·7	13·8	41·5	6·2
B.L. × Chev.	II	5679	62·5	10·7	13·0	23·7	11·9	3007	61·7	19·0	11·3	30·3	6·9
Cheviot	III	5362	58·5	14·6	13·5	28·1	12·0	3007	53·0	25·3	12·9	38·2	6·8
Oxford × B.L. Chev.	IV	5459	60·6	8·8	13·3	22·1	14·7	2432	64·3	13·2	10·4	23·6	9·7
Suffolk × B.L. Chev.	V	6014	60·9	13·1	11·8	24·9	12·8	3235	55·3	31·2	5·3	36·5	7·6
Lambs													
Southdown × B.L. Chev.	VI	3417	61·0	15·2	10·8	26·0	11·9	2034	62·5	20·6	10·0	30·6	6·8
Suffolk × B.L. Chev.	VII	3389	64·2	9·7	9·6	19·3	15·3	2340	65·5	16·3	10·0	26·3	8·4
Oxford × B.L.-Chev.	VIII	3515	58·1	11·8	12·9	24·7	15·9	1981	58·5	19·1	12·8	31·9	10·3
Blackfaced	IX	3162	58·2	11·6	13·2	24·8	13·7	1990	53·9	21·6	13·9	35·5	8·4
B.L. × Chev.	X	3142	63·0	9·9	8·3	18·3	16·2	1749	60·3	19·2	10·3	29·5	9·4
B.L. × Blackfaced	XI	3037	62·0	11·0	9·3	20·3	15·5	1843	58·1	23·0	10·3	33·3	9·0
Cheviot	XII	3226	62·7	10·5	12·5	23·0	13·3	1698	60·5	17·6	15·4	33·0	8·8
Uruguay	XIII	2945	58·0	11·7	10·9	22·6	16·4	1632	50·4	24·1	13·7	37·8	10·0
Southdown × Romney	XIV	3397	52·1	17·0	15·4	32·4	11·1	2038	48·7	28·1	15·2	43·3	5·4
B.L. × Iceland	XV	3278	62·0	11·5	7·7	19·2	16·4	2118	60·0	18·0	9·8	27·8	10·0
Iceland	XVI	3101	61·8	8·0	7·0	15·0	17·3	1810	61·3	17·0	10·2	27·2	9·1

Table 88 (*continued*)

Breed	No	Pelvis						Legs					
		Total wt. g.	Muscle	Subcutaneous fat	Fat inter-muscular	Total fat	Bone	Total wt. g.	Muscle	Subcutaneous fat	Fat inter-muscular	Total fat	Bone
Hoggets													
B.L. × Blackfaced	I	3095	44·7	31·5	11·6	43·1	11·0	5024	65·1	14·3	5·7	20·0	12·2
B.L. × Chev.	II	2999	50·9	25·9	10·8	36·7	10·8	5465	67·6	10·6	5·8	16·4	12·6
Cheviot	III	2925	44·7	31·5	10·6	42·1	12·0	5422	64·7	14·4	5·7	20·1	12·4
Oxford × B.L.-Chev.	IV	2733	53·6	21·4	11·0	32·4	13·2	5590	67·0	8·9	6·5	15·4	14·3
Suffolk × B.L.-Chev.	V	2967	49·8	28·7	7·7	36·4	13·4	6085	68·5	11·0	4·9	15·9	12·5
Lambs													
Southdown × B.L.-Chev.	VI	1898	50·6	26·2	11·1	37·3	11·0	3755	67·9	14·0	3·9	17·9	12·2
Suffolk × B.L.-Chev.	VII	1842	54·1	21·3	10·5	31·8	14·1	4063	69·9	9·3	3·6	12·9	14·2
Oxford × B.L.-Chev.	VIII	1773	48·4	24·4	11·3	35·7	16·2	3930	65·1	11·6	4·6	16·2	15·6
Blackfaced	IX	1484	46·8	24·2	14·0	38·2	13·7	3639	65·6	13·8	4·5	18·3	12·6
B.L. × Chev.	X	1663	49·1	22·8	11·2	34·0	15·7	4008	68·8	11·2	3·5	14·7	13·3
R.L. × Blackfaced	XI	1747	46·6	28·4	9·9	38·3	14·9	3955	67·7	13·5	3·4	16·9	12·6
Cheviot	XII	1725	53·6	22·8	11·6	33·8	12·8	3678	68·5	11·7	4·2	15·9	12·9
Uruguay	XIII	1706	39·4	30·8	11·5	42·4	14·4	3627	65·8	11·2	4·1	15·2	14·6
Southdown × Romney	XIV	1662	37·0	30·4	15·8	46·2	11·9	3977	58·9	19·3	6·1	25·5	10·2
B.L. × Iceland	XV	1716	50·1	20·6	12·1	32·7	14·9	3800	68·4	10·0	3·5	13·5	14·0
Iceland	XVI	1987	50·8	19·9	11·2	31·1	13·0	3846	66·0	7·1	3·6	10·7	15·7

Table 88 (continued)

All joints (head, feet, kidneys and kidney-fat excluded)

Breed	No.	Total wt. g.	Muscle	Sub-cutaneous fat	Inter-muscular fat	Total fat	Bones	Tendon, etc.	Loss
Hoggets									
B.L. × Blackfaced	I	24405	52·2	19·5	14·4	33·9	11·9	1·4	0·6
B.L. ×Chev.	II	25373	58·9	15·5	11·4	26·9	12·0	1·6	0·6
Cheviot	III	25245	53·5	18·8	13·7	32·5	12·0	1·4	0·6
Oxford × B.L.-Chev.	IV	24413	58·1	11·7	13·4	25·1	14·4	2·1	0·3
Suffolk × B.L. Chev.	V	27106	56·6	18·5	10·4	28·9	13·0	1·6	−0·1
Lambs									
Southdown × B.L.-Chev.	VI	16138	58·8	17·3	11·1	28·4	11·8	1·6	−0·6
Suffolk × B.L.-Chev.	VII	17368	61·4	12·8	10·9	23·7	13·9	1·8	−0·8
Oxford × B.L.-Chev.	VIII	16614	55·4	15·3	12·8	28·1	15·4	2·2	−1·0
Blackfaced	IX	15545	54·3	15·2	14·8	30·0	13·0	2·1	0·6
B.L. × Chev.	X	16474	59·1	13·8	10·5	24·3	14·3	2·0	0·2
B.L. × Blackfaced	XI	16208	56·9	15·9	11·8	27·7	13·7	1·8	−0·1
Cheviot	XII	15852	58·9	13·6	13·5	27·1	12·8	2·0	−0·8
Uruguay	XIII	15360	51·7	16·9	14·1	31·0	14·5	2·4	−0·8
Southdown × Romney	XIV	17547	47·4	21·0	17·0	38·0	10·1	1·5	0·4
B.L. × Iceland	XV	16451	58·2	13·1	10·9	24·0	14·5	1·6	3·0
Iceland	XVI	16508	58·3	11·2	10·5	21·7	14·5	1·9	3·6

relatively high percentage of the weight of a joint, because the latter contains little muscle and/or fat, but not because it actually contains a larger amount of bone compared with the same joint in other breeds. However, the percentage composition is of great importance from the butcher's and consumer's point of view as it measures the proportions of edible meat (muscle and fat) compared with the waste (bone and tendon). The bone in the whole carcass varies from 10·1 to 15·4% of the total weight in lambs but from 11·9 to 14·4 % in the hoggets. The breed differences are great, the percentage weight of bone showing a difference range of 50%. There is a considerable variation between joints in bone. The loin contains by far the least bone, varying from 5·4 to 10·3% in the lambs, and 6·2 to 9·7 % in the hoggets. The thorax contains the largest proportion of bone with an average of 14·8% in the lambs. In all the joints except loin, the nature of the joints affects the proportion of bone much less than breed.

At 4·5 months the Southdown × Romney has the smallest proportions of bone in all joints. This is partly due to its very light bones as well as its high state of fatness. The Southdown × B.L.-Cheviot comes second in this respect. The Oxford × B.L.-Cheviot has the largest proportions of bone in the total carcass and in all the joints but shoulders and legs, where the Iceland has a still higher percentage. In the hoggets the Oxford × B.L.-Cheviot has the highest percentage bone in all joints except the neck and pelvis, where it is exceeded by the Suffolk × B.L.-Cheviot. The other breeds do not differ very much in this respect.

The percentage of muscle is highest in the legs, followed by the shoulders and loin. The other joints do not differ greatly between themselves in the lambs. In the hoggets the neck has a higher percentage of muscle than the thorax and the pelvis. The proportions of muscle are highest in the lean lambs (Suffolk × B.L.-Cheviot and B.L. × Blackfaced) but lowest in the fat ones (Southdown × Romney, Uruguay and B.L. × Blackfaced). In the hoggets this same condition exists, the B.L. × Cheviot and Oxford × B.L.-Cheviot having the largest percentage amount.

The relative amount of subcutaneous and intermuscular fat varies in different joints. The neck contains much more intermuscular fat than subcutaneous fat in the lambs, but in the hoggets there is approximately the same amount of both kinds. In the thorax this difference is smaller than in the neck, though in most breeds there is more intermuscular than subcutaneous fat. The Oxford × B.L.-Cheviot hogget has particularly poorly developed subcutaneous fat in the thorax. The shoulders contain approximately the same amount of subcutaneous and inter-

muscular fat, except in the Oxford × B.L.-Cheviot which has much less of the former. In loin, legs and pelvis there is much less intermuscular than subcutaneous fat. The latter makes up more than half of the total fat in the carcass. This indicates that good development of subcutaneous fat is more important than is intermuscular fat. All the joints which contain relatively more of the latter constitute the cheaper cuts (see following paragraph). Indeed it appears that too much intermuscular fat may greatly lower the value of some joints (neck and thorax) before the subcutaneous fat becomes excessive. In the total carcass the Mountain breeds (Iceland, Cheviot and Blackfaced lambs) have relatively less subcutaneous fat than intermuscular fat as compared with Down and Border Leicester crosses. The legs are inclined to contain a very low percentage of fat. This may in late-developing or large breeds at light weights greatly reduce the quality of the carcass. In the lambs the Iceland has only 10·7% fat in the legs, the Suffolk × B.L.-Cheviot 12·9%, which is too low. On the other hand the short-legged breeds contain much more fat in the leg. The Cheviot 15·9%, B.L. × Blackfaced 16·9%, Blackfaced 18·3%, Southdown × B.L.-Cheviot 17·9% and Southdown × Romney 25·5%. In the hoggets the same trend is obvious. The Cheviot and B.L. × Blackfaced have 20% of fat in the legs, the B.L. × Cheviot 16·4%, but the Suffolk and Oxford crosses only 15·9 and 15% respectively. This is a further proof of the detrimental effects of long bones as compared with short ones.

The actual amount of tendon, glands etc. in each joint is given in Appendix III. The legs contain most tendon followed by the shoulders and neck. This is due to the large amount of tendons surrounding the tarsals and carpals as well as the strong tendons by which the large muscles of the limbs are attached to the bones. The neck contains more glands than any other joint. The thorax, loin and pelvis contain hardly any "waste" tissue, apart from the bones, but the spinal cord. Table 88 shows the percentage tendon, glands etc. in the total carcass (less head, feet and kidneys) in the different breeds. It is greatest in the long and heavy-boned breeds, viz. Uruguay and Oxford × B.L.-Cheviot, both as lamb and hogget. The Southdown crosses have the lowest percentage of tendon. The hoggets have relatively less tendon than the lambs of the same breeds.

C. Comparative value of different joints

The effect of breed and carcass weight on the price per stone (8 lb.) of the carcass has been studied by Hammond & Murray (1934). They found that the price fell with increase in carcass weight, but at different

rates in the various breeds (see Text-fig. 18). They also demonstrated the fact that in times of low prices the buyers differentiate against a heavy carcass more than in times of high prices. Hirzel (1936) studied in different breeds the effects of carcass quality on the fall in price with weight increase demonstrated by Hammond & Murray. At light weights late-maturing (Blackfaced and Welsh) breeds command a lower price per lb. than early-maturing (Southdown) because the former are too lean at these weights. With an increase in weight the early-maturing breeds fall in value more rapidly than the late-maturing ones owing to excessive fat
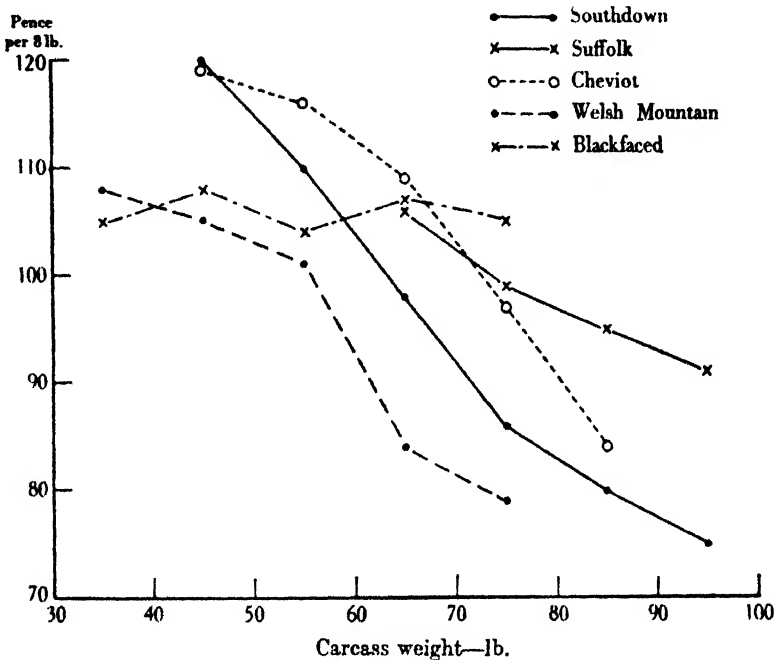
Text-fig. 18. Prices for carcasses of different weights in various breeds of sheep.
(From Hammond & Murray, 1934.)

development. Indeed, in the Blackface (Text-fig. 18) the price per stone does not fall with weight, indicating that the improved quality with weight increase does counterbalance the harmful effect on price incurred by the weight increase. Hammond (1937 b) illustrates how quality and weight affected the prices of imported frozen Argentine mutton and lamb in the London Meat Market during the winter of 1937 (see Text-fig. 19). There is a great difference due to quality, but weight of carcass is however of still greater importance. The fact that a pound of meat is worth more in some regions of the carcass than others has been referred to several times above. It is clear from this study that some difference in price per pound is warranted because of the difference in composition of

the various joints. Hammond (1932) studied thoroughly the various factors which affected the relative price per lb. in different joints. He found that the price was little dependent on the food value of the joint
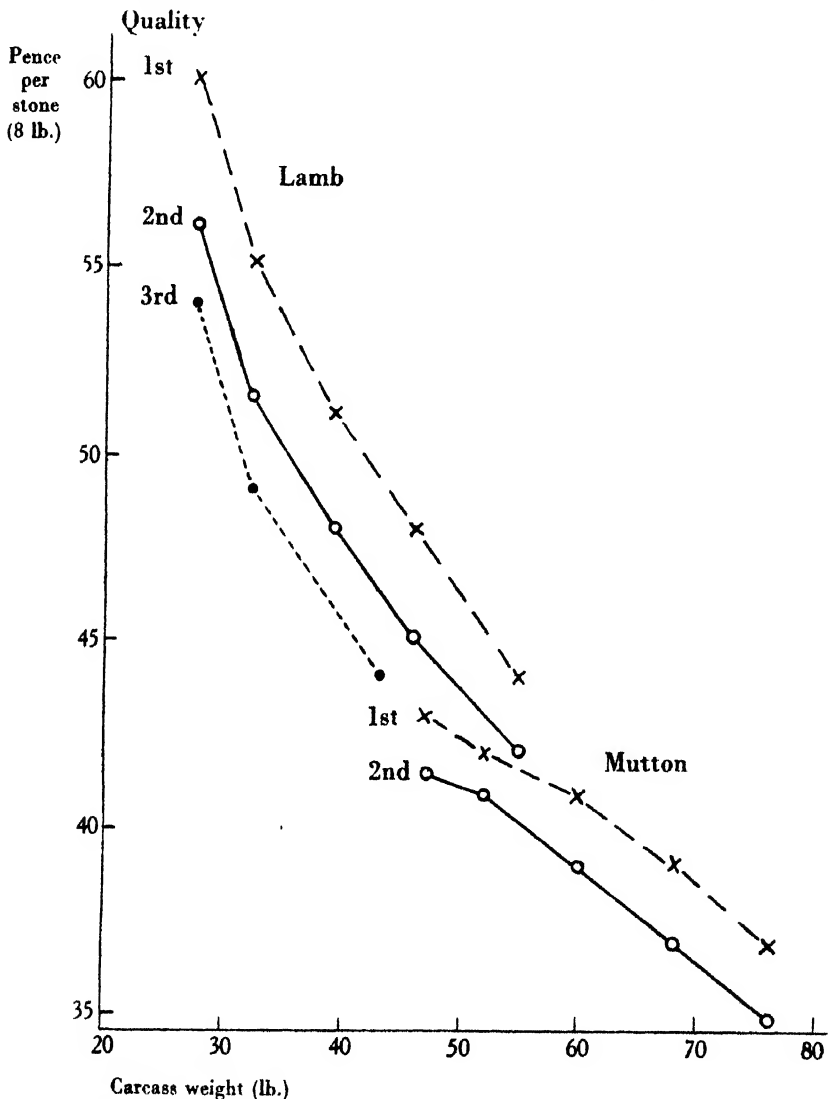
Text-fig. 19. Prices of imported (Argentine) frozen mutton and lamb, Feb. 1937.
(From Hammond, 1937*b*.)

and quotes Edinger (1925), who found in beef that the relative food values of the different joints do not correspond to their market prices, the cost of the lean meat (muscle) from the loin and rib being 150% higher in fat than in thin steers. Hammond concluded that the price of a joint is to a large extent fixed by the proportions of meat (muscle and fat) to the

bone that it contains, and that the estimate so formed will be lowered by variation (either too low or too high) in the proportion of fat to muscle present. The way in which the joint can be cooked appears to affect its economic value. Those parts used for roasting (loin, pelvis and legs) are more expensive per lb. relative to their composition than those parts used for stewing or boiling (neck and flank).

Table 89. *Prices of different joints*

Retail price of whole joint in pence per lb. as quoted by Mr William Orr, Edinburgh.

Joint	Price per lb.
Neck	8
Shoulders	12
Fore-end of thorax (five ribs), lower part of ribs and flank	12
Rib cutlets (posterior upper half of thorax)	23
Loin	23
Chump	18
Legs	19

To give an idea of the relative price per lb. in different joints in Scotland at present, we have obtained, through the kindness of Mr William Orr, the retail prices per lb. of different regions of the carcass of first quality Scotch lamb (see Table 89). We have not jointed our animals exactly in the same way as is done commercially in Scotland. In commerce the posterior upper half of the eight last ribs are sold at the same price as the loin (rib cutlets), but is included in the thorax in our case. This increases the value per lb. in the latter from $12d.$ to approximately $15d.$ per lb. The chump corresponds closely to our pelvis. It will be realized that these differences will be less marked in meat of inferior quality, because in such cases the high prices may not be obtainable for the hindquarters. If the loin and legs are unsuitable for roasting the value of the carcass will consequently be greatly reduced, as the cheaper cuts of an inferior quality carcass will not even be worth as much as the corresponding cuts of prime quality. From the prices quoted in Table 89 and the relative weights of different joints in the carcass (see § III. A) it is obvious that, regardless of quality, the Southdown × B.L.-Cheviot carcass is worth more per lb. to the butcher than the Border Leicester × Cheviot carcass owing to the relative weight differences of the joints. The latter has 554 g. heavier neck. 324 g. heavier thorax, 275 g. lighter shoulders, 285 g. lighter loin, 235 g. lighter pelvis and 253 g. heavier legs than the former, the total carcass of the former being 336 g. lighter than that of the latter. In addition the B.L. × Cheviot cross is of much poorer quality, contains more bone, has poorer Shape Index of eye muscle and too thin fat cover on the loin. This example serves to illustrate the

economic importance of good conformation and quality of the carcass and several other comparable examples can be seen in our data.

SUMMARY

It is not intended to present a detailed summary of the many points arising out of this investigation. The following represents merely a brief statement of the field covered and the major features emerging.

1. Complete anatomical dissection of eleven wether lambs at approximately 4·5 months old and 40 lb. carcass weight and five wether hoggets at approximately 13 months and 60 lb. carcass weight provided material for a comparative study of the anatomical composition and characters of different breeds and crosses of which the individuals concerned were selected as representative.

2. In both lambs and hoggets this study confirms the picture presented by the statistical comparison based on carcass measurements of the same breeds and crosses at constant weight described and discussed in Part II.

3. The breed differences in the relative development of the different regions of the body and the relative development of the major tissues, bone, muscle and fat in different joints and the total carcass have been studied in relation to carcass quality.

4. From the differential development of the different parts and tissues of the body in the various breeds and crosses, the concept of early and late development as a fundamental factor in meat production is demonstrated.

5. The proportional development of the various parts of the body and its major tissues in lambs and hoggets is compared. Regions of an intermediate rate of development are relatively best developed in the hoggets. In the total carcass, bone has increased least, muscle only slightly more and fat most, with an increase in age from 4·5 to 13 months and body weight from 40 to 60 lb. This is in line with the order of the development of the tissues.

6. The differential effect upon differentially developing tissues of the plane of nutrition is advanced as a major factor influencing the relative differences between lambs and hoggets.

7. Variations, affecting the value of the animal for meat production, in the number of vertebrae in the different anatomical regions have been described.

8. The bearing of the many factors discussed and principles elucidated

upon practical problems of lamb and mutton production has been considered.

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REFERENCES

BERGE, S. (1936). *Meld. Norg. LandbrHøisk.* **16**, 547.
BERGER, J. (1920). Inaug. Diss. Vet. med. Fak., Univ. Bern.
CHIRVINSKY, N. P. (1909). *Politeknich. Inst.* II, Kiev.
DIFFLOTH, N. P. (1908). *Zootechnie spéciale.* Paris.
EDINGER, A. T. (1925). *Res. Bull. Mo. agric. Exp. Sta.* no. 83.
EWART, J. (1878). *Meat Production.* London.
FISHER, R. A. (1936). *Statistical Methods for Research Workers*, 6th ed. Edinburgh.
HALL, A. D. (1936). Ernle's *English Farming, Past and Present*, 5th ed. London.
HALL, L. D. (1910). *Bull. Ill. agric. Exp. Sta.* no. 147.

HAMMOND, J. (1921). *J. agric. Sci.* **11**, 367.

—— (1932). *Growth and Development of Mutton Qualities in the Sheep.* Edinburgh.

—— (1936). *Neue Forschungen in Tierzucht. u. Abstammungslehre.* Festschrift Prof. U. Duerst, Bern.

—— (1937*a*). *Nord. JordbrForskn.* Hefte 1-2, pp. 24–37.

—— (1937*b*). *Rep. 36th Int. Conf. Nat. Sheep Breed. Ass.* pp. 6–26.

—— (1937*c*). *Growth in the Sheep* (in the Press).

HAMMOND, J. & MURRAY, G. N. (1934). *J. agric. Sci.* **24**, 233.

HANKINS, O. G. & ELLIS, N. R. (1934). *J. agric. Res.* **48**, 257.

HARRIS, H. A. (1938). Personal communications.

HIRZEL, R. (1936). Factors affecting quality in mutton with special reference to the proportions of muscle, fat and bone. Diss. Pretoria University; and (1940) *Onderstepoort J. vet. Sci.* **12**, No. 2.

KRONACHER, C. & HOGREVE, F. (1936). *Z. Zucht.* B, **35**, 161.

LAWES, J. B. & GILBERT, J. A. (1858). *Proc. roy. Soc.* **9**, 348.

LEIGHTON, G. R. & DOUGLAS, L. M. (1910). *The Meat Industry and Meat Inspection*, **3**. London.

McMEEKAN, C. P. (1938). Growth and development in the pig. Ph.D. Thesis Cambridge University.

MEEK, A. (1901). *Veterinarian, Lond.*, **74**, 171.

MILLIKAN, G. A. (1936). *J. Physiol.* **87**, 38*P*.

NATHUSIUS, H. VON (1880). *Vortrage über Viehzucht und Rassenkenntniss.* II. *Schafzucht.* Berlin.

NEEDHAM, J. (1926). *Physiol. Rev.* **6**, 1.

ROBERTSON, G. C. A. (1932). Royal Institute of International Affairs. *World Agriculture.* Oxford.

—— (1936). *Rep. Leeds Coun. agric. Educ.* no. 183.

SHAW, A. M. (1929-30). *Sci. Agric.* **10**, 23, 690.

SNEDECOR, G. W. (1934). *Calculations and Interpretation of Analysis of Variance and Covariance.* Ames, Iowa.

TROWBRIDGE, P. F., MOULTON, C. R. & HAIG, L. D. (1918-23). *Res. Bull. Mo. agric. Exp. Sta.*, Nos. 28, 30, 43, 54, 55, 61.

WATERS, H. J. (1909). *Proc. Soc. Prom. Agric. Res.* 13th meeting, p. 70.

APPENDIX I

Details of origin, age and weight of animals used in the dissection (weights in lb.)

No.	Breed	Sex	Age mo.	Origin	Date of slaughter	Place of slaughter	Live wt. lb.	Wt of carcass -head warm	Wt of cold carcass -head 12 hr. after killing	Date of dissection	Place of dissection	Wt of carcass -head when cut up	Loss from time of killing till cut up	Wt of carcass -head	% cold dressed carcass wt.	Loss during dissection
I	B.L. × Blackfaced	♂	13	Fife, Scot	4 v 37	Edin.	116	64.5	63.0*	5 v 37	Camb.	61.0	3.5	56.53	48.7	0.70
II	B.L. × Chev.	♂	13	Lothians, Scot	4 v 37	Edin	113	66.0	64.0*	5 v 37	Camb.	62.3	3.7	57.84	51.2	0.38
III	Cheviot	♂	13	Borders, Scot.	10 v 37	Edin	109	66.0	64.5	11 v 37	Camb.	62.7	3.3	58.40	53.6	0.20
IV	Oxford × B.L.-Chev.	♂	13	S.E. Scot	11 v 37	Edin.	112	65.5	63.5	15 v 37	Camb.	60.3	5.2	55.70	49.7	0.10
V	Suffolk × B.L.-Chev	♂	13	Lothians, Scot	13 v 37	Edin.	—	68.0	65.0	17 v 37	Camb.	66.7	1.3	61.00	—	−0.06
VI	Southdown × B.L.-Chev	♂	4½	Borders, Scot	4 viii 37	Edin.	75	43	42.0*	5 viii 37	Camb.	40.31	2.7	37.00	49.3	−0.28
VII	Suffolk × B.L.-Chev	♂	4½	S E Scot.	4 viii 37	Edin.	79	46	44.5*	6 viii 37	Camb.	42.8	3.2	39.34	49.8	−0.46
VIII	Oxford × B.L.-Chev	♂	4½	Mid-Loth, Scot.	4 viii 37	Edin	76	44.5	43.0*	7 viii 37	Camb	41.5	3.0	38.00	50.0	−0.44
IX	Blackfaced	♂	4½	E. Lothians, Scot.	1 ix 37	Edin.	76	44.0	42.5	2 ix 37	Camb.	40.0	4.0	36.20	47.0	0.30
X	B.L. × Chev.	♂	4½	Peeblesshire, Scot	1 ix 37	Edin.	80	44.5	43.0*	2 ix 37	Camb	41.3	3.5	37.72	47.2	0.10
XI	B.L. × Blackfaced	♂	4½	Fife, Scot	1 ix 37	Edin	75	44.5	43.0*	3 ix 37	Camb.	40.3	4.2	37.24	49.6	−0.04
XII	Cheviot	♂	4½	Mid-Loth, Scot	1 ix 37	Edin.	71	44.0	43.0	3 ix 37	Camb	40.0	4.0	36.80	51.8	−0.28
XIII	Uruguay†	♂	4½	Uruguay	—	—	—	—	—	5 ix 37	Camb.	—	—	35.04	—	0.19
XIV	Southdown × Romney†	♂	4½	Longburn, N.Z	—	—	—	—	—	7 ix 37	Camb.	—	—	40.44	—	1.22
XV	B.L. × Iceland	♀	1½	Bardardal, Iceland	24 ix 37	Akureyri	84	44.0	43.0	26 ix 37	Akureyri	41.1	2.9	37.42	44.5	0.68
XVI	Iceland†	♀	4½	Oxnadal, Iceland	23 ix 37	Akureyri	90	44.5	43.5	30 xi 37	Camb.	42.8	1.7	38.75	43.0	1.36
XVII	Southdown × Merino†	?	4½	W Australia	—	—	—	—	—	1 vii 37	Camb.	—	—	19.84	—	—

* Estimated from weight of warm † Frozen carcasses. ‡ ½ carcass.

APPENDIX II

Carcass measurements of the sheep used for dissection (linear measurements, mm.)

| Breed | No. of sheep | F | G | H | I | K | L | M | R | T | N | Th | A | B | C | D | J | V | Y | Z | Left fore-cannon | | | | Colour of muscle |
																					Length	Min. cir.	Wt.	$\frac{Wt.}{Length} \times 100$	
Hoggets																									
B.L. × Blackfaced	I	272	253	140	475	705	625	127	189	221	185	—	57.0	31.0	7.0	9.0	15.0	13.0	11.0	28.5	127	49	47.6	37.5	10
B.L. × Chev.	II	280	254	147	495	720	660	129	193	228	190	—	61.0	35.5	3.5	4.0	13.5	15.0	5.0	28.0	129	50	51.5	39.9	9
Cheviot	III	258	250	144	465	700	648	124	185	211	250	—	65.0	27.0	6.5	4.0	14.0	11.0	8.0	28.5	123	50	48.9	39.7	9
Oxford × B.L.-Chev.	IV	298	250	144	493	730	658	135	195	230	280	300	69.5	27.0	3.0	4.0	8.0	14.5	4.5	28.5	133	55	59.8	45.0	9
Suffolk × B.L.-Chev.	V	274	252	146	495	735	655	132	193	224	240	292	64.0	34.5	5.0	4.0	16.5	14.0	9.5	28.0	132	51	63.0	47.7	8
Lambs																									
Southdown × B.L.-Cher.	VI	226	219	125	420	565	548	107	155	187	130	255	55.5	29.5	5.0	6.0	14.0	13.0	5.0	20.0	106	44	35.0	33.0	10
Suffolk × B.L.-Chev.	VII	257	230	119	430	660	604	117	175	200	170	261	63.0	24.5	3.0	3.5	13.5	13.0	4.0	24.0	113	45	43.0	38.0	11
Oxford × B.L.-Chev.	VIII	273	220	121	425	630	602	126	175	207	150	260	55.5	24.5	3.0	3.0	10.5	11.0	4.0	24.0	123	47	49.0	39.8	9
Blackfaced	IX	219	217	117	400	618	578	113	169	193	158	253	58.0	25.5	2.5	2.0	7.5	12.0	3.0	23.0	110	48	38.6	35.1	10
B.L. × Chev.	X	260	210	124	415	640	585	122	176	206	162	270	59.0	26.0	3.0	4.0	8.0	11.0	4.0	22.5	122	47	43.2	35.4	8
B.L. × Blackfaced	XI	252	224	157	425	635	590	115	173	194	140	257	57.0	29.5	1.0	2.0	10.5	12.0	5.0	25.5	114	45	39.2	34.4	11
Cheviot	XII	227	215	117	400	600	550	110	161	184	135	235	55.5	30.0	3.5	3.0	10.0	12.5	3.0	24.0	107	45	36.2	33.8	10
Uruguay	XIII	278	196	114	410	610	575	—	176	205	128	281	56.0	23.0	4.0	3.0	9.5	10.0	3.5	24.0	—	—	—	—	12
Southdown × Romney	XIV	214	230	122	425	605	530	—	154	178	137	266	51.0	27.0	5.5	8.5	16.5	18.5	6.0	19.0	—	—	—	—	9
B.L. × Iceland	XV	262	223	121	410	645	600	118	179	205	150	263	58.0	24.5	4.0	1.0	9.0	12.5	3.5	25.0	117	46.0	42.0	35.9	11
Iceland	XVI	292	233	116	435	640	595	134	185	225	168	280	56.0	24.5	2.0	1.0	7.0	10.0	2.5	28.0	133	45.0	45.0	33.8	11
Southdown × Merino	XVII	256	120	138	—	600	554	—	165	197	138	266	57.0	23.0	5.0	6.0	13.0	11.5	—	—	—	—	—	—	12

APPENDIX III

Actual weights of muscle, fat, bone and tendon in the different joints of carcass (gm.)

Tissue	Total	Muscle	Subcutaneous fat	Fat between muscles	Bone	Tendon glands and waste	Loss
I. B.L. × Blackfaced. Wether 13 months							
Neck	1915	950	303	296	275	61	30
Thorax	6047	2612	1233	1288	848	27	39
Shoulder right: Shoulder	2722	1373	320	472	319	54	7
Arm		161		16			
Shoulder left: Shoulder	2647	1320	392	368	322	41	27
Arm		163		14			
Loin	2955	1505	818	408	184	11	29
Pelvis	3095	1385	974	359	339	5	33
Leg right: Thigh	2525	1327	370	120	304	72	− 7
Leg		305		34			
Leg left: Thigh	2499	1324	349	102	308	72	0
Leg		315		29			
Total joints	24405	12740	4759	3506	2899	343	158
Kidneys	122						
Kidney fat	839						
Diaphragm	137						
Total carcass	25503						
Head	2035						
Feet (4)	910						
Cold carcass: head and feet	25665						
II. B.L. × Chev. Wether 13 months							
Neck	2003	1154	255	229	291	86	− 12
Thorax	6230	3169	1132	943	868	46	72
Shoulder right: Shoulder	2775	1533	299	327	338	55	− 7
Arm		201		29			
Shoulder left: Shoulder	2894	1610	308	363	338	52	− 2
Arm		204		21			
Loin	3007	1854	570	342	208	15	18
Pelvis	3009	1527	778	323	325	8	48
Leg right: Thigh	2785	1555	310	119	342	65	16
Leg		332		46			
Leg left: Thigh	2680	1490	269	115	347	83	24
Leg		316		36			
Total joints	25383	14945	3921	2893	3057	410	157
Kidneys	142						
Kidney fat	567						
Diaphragm	160						
Total carcass	26242						
Head	2033						
Feet (4)	1015						
Cold carcass: head and feet	26257						

III. Cheviot. Wether 13 months

Tissue	Total	Muscle	Subcutaneous fat	Fat between muscles	Bone	Tendon glands and waste	Loss
Neck	2218	1119	333	412	276	54	24
Thorax	6310	2842	1160	1311	891	51	46
Shoulder right: Shoulder	2600	1358	368	320	323	36	− 5
Arm		180		20			
Shoulder left: Shoulder	2763	1420	413	362	323	35	7
Arm		180		23			
Loin	3007	1594	762	387	206	34	24
Pelvis	2925	1308	920	311	352	5	29
Leg right. Thigh	2737	1476	408	107	332	76	4
Leg		305		29			
Leg left. Thigh	2685	1431	374	120	341	50	20
Leg		295		54			
Total joints	25245	13508	4747	3456	3044	341	149
Kidneys	135						
Kidney fat	1087						
Diaphragm	107						
Total carcass	26574						
Head	1956						
Feet (4)	911						
Cold carcass: head and feet	26514						

IV. Oxford × B.L.-Chev. Wether 13 months

Tissue	Total	Muscle	Subcutaneous fat	Fat between muscles	Bone	Tendon glands and waste	Loss
Neck	2344	1230	337	337	337	107	− 4
Thorax	5860	2836	639	1292	983	44	66
Shoulder right: Shoulder	2705	1467	220	347	401	56	6
Arm		188		20			
Shoulder left. Shoulder	2754	1502	262	332	400	47	− 10
Arm		194		27			
Loin	2432	1565	321	253	235	58	-
Pelvis	2733	1464	585	300	360	6	18
Leg right: Thigh	2810	1576	232	117	400	77	− 1
Leg		326		53			
Leg left: Thigh	2780	1525	266	126	400	115	− 5
Leg		317		36			
Total joints	24418	14190	2862	3270	3516	510	70
Kidneys	143						
Kidney fat	561						
Diaphragm	184						
Total carcass	25306						
Head	2069						
Feet (4)	1131						
Cold carcass: head and feet	25281						

V. Suffolk × B.L.-Chev. Wether 13 months

Tissue	Total	Muscle	Subcutaneous fat	Fat between muscles	Bone	Tendon glands and waste	Loss
Neck	2255	1177	445	205	353	77	− 2
Thorax	6550	3056	1241	1206	1016	33	− 2
Shoulder right. Shoulder	2975	1595	370	360	381	62	− 13
Arm		203		17			
Shoulder left: Shoulder	3039	1661	420	313	376	52	− 6
Arm		205		18			
Loin	3235	1790	1008	172	247	21	− 3
Pelvis	2967	1477	852	229	398	8	3
Leg right: Thigh	3035	1723	291	158	380	101	− 4
Leg		361		25			
Leg left: Thigh	3050	1711	378	91	382	89	—
Leg		377		22			
Total joints	27106	15336	5005	2816	3533	443	− 27
Kidneys	142						
Kidney fat	655						
Diaphragm	109						
Total carcass	28012						
Head	2290						
Feet (4)	1168						
Cold carcass: head and feet	28010						

Tissue	Total	Muscle	Subcutaneous fat	Fat between muscles	Bone	Tendon glands and waste	Loss
VI. Southdown × B.L.-Chev. Wether 4·5 months							
Neck	1145	607	160	190	157	37	− 6
Thorax	3889	2015	669	674	542	36	47
Shoulder right: Shoulder	1698	885	258	183	202	40	17
Arm		138		9			
Shoulder left: Shoulder	1719	923	260	170	204	30	15
Arm		138		9			
Loin	2034	1271	418	204	138	12	− 9
Pelvis	1898	960	498	210	209	17	4
Leg right: Thigh	1893	1058	251	60	233	42	− 10
Leg		238		21			
Leg left: Thigh	1862	1015	274	50	226	51	− 8
Leg		240		14			
Total joints	16138	9488	2788	1794	1911	265	− 108
Kidneys	89						
Kidneys fat	459						
Diaphragm	116						
Total carcass	16802						
Head	1477						
Feet (4)	657						
Cold carcass: head and feet	16793						
VII. Suffolk × B.L.-Chev Wether 4·5 months							
Neck	1603	886	189	273	226	40	− 11
Thorax	4131	2228	553	716	642	28	36
Shoulder right: Shoulder	1693	946	162	152	268	42	− 26
Arm		139		10			
Shoulder left: Shoulder	1696	952	168	155	249	41	− 17
Arm		140		8			
Loin	2340	1533	380	235	197	10	− 15
Pelvis	1842	997	392	193	260	7	− 7
Leg right: Thigh	2009	1110	169	58	292	74	− 8
Leg		292		22			
Leg left: Thigh	2054	1180	208	53	285	79	− 24
Leg		259		14			
Total joints	17368	10662	2221	1889	2419	321	− 144
Kidneys	115						
Kidney fat	320						
Diaphragm	124						
Total carcass	17927						
Head	1560						
Feet (4)	807						
Cold carcass: head and feet	17860						
VIII. Oxford × B.L.-Chev. Wether 4·5 months							
Neck	1439	716	176	272	223	57	− 5
Thorax	3976	1868	681	770	664	37	− 44
Shoulder right: Shoulder	1799	909	211	232	276	46	− 32
Arm		142		15			
Shoulder left: Shoulder	1716	852	203	195	283	51	− 20
Arm		139		13			
Loin	1981	1159	378	253	205	10	− 24
Pelvis	1773	858	432	200	287	10	− 14
Leg right: Thigh	2008	1070	247	80	305	65	− 12
Leg		235		18			
Leg left: Thigh	1922	1019	209	66	309	86	− 20
Leg		236		17			
Total joints	16614	9203	2537	2131	2552	362	− 171
Kidneys	116						
Kidney fat	426						
Diaphragm	112						
Total carcass	17268						
Head	1604						
Feet (4)	899						
Cold carcass: head and feet	17240						

Tissue	Total	Muscle	Subcu- taneous fat	Fat between muscles	Bone	Tendon glands and waste	Loss
IX. Blackfaced. Wether 4·5 months							
Neck	1460	647	172	366	197	63	15
Thorax	3810	1799	537	863	562	34	15
Shoulder right: Shoulder	1592	790	180	184	225	35	36
Arm		133		9			
Shoulder left: Shoulder	1570	787	186	218	209	41	− 10
Arm		131		8			
Loin	1990	1073	430	276	167	17	27
Pelvis	1484	694	359	208	204	3	16
Leg right: Thigh	1858	1008	251	80	227	64	—
Leg		214		14			
Leg left: Thigh	1781	948	253	51	230	67	− 2
Leg		217		17			
Total joints	15545	8441	2368	2294	2021	324	97
Kidneys	92						
Kidney fat	632						
Diaphragm	120						
Total carcass	16389						
Head	1602						
Feet (4)	719						
Cold carcass: head and feet	16428						
X. B.L. ᴥ Cheviot. Wether 4·5 months							
Neck	1699	888	206	319	200	68	18
Thorax	4213	2230	599	641	693	33	17
Shoulder right: Shoulder	1548	837	143	125	257	41	− 6
Arm		144		7			
Shoulder left: Shoulder	1594	857	169	123	252	40	0
Arm		146		7			
Loin	1749	1054	335	180	165	13	2
Pelvis	1663	816	379	187	261	9	11
Leg right: Thigh	2065	1176	244	50	267	70	− 4
Leg		249		13			
Leg left: Thigh	1943	1088	206	65	266	61	0
Leg		245		12			
Total joints	16474	9730	2281	1729	2361	335	38
Kidneys	104						
Kidney fat	412						
Diaphragm	128						
Total carcass	17118						
Head	1495						
Feet (4)	750						
Cold carcass: head and feet	17125						
XI. B.L. ᴥ Blackfaced. Wether 4·5 months							
Neck	1419	675	207	293	195	46	3
Thorax	4207	2108	590	841	629	32	7
Shoulder right: Shoulder	1501	803	165	130	234	36	− 2
Arm		125		10			
Shoulder left: Shoulder	1536	829	168	135	237	40	− 6
Arm		125		8			
Loin	1843	1071	424	189	166	10	− 17
Pelvis	1747	814	497	172	260	6	− 2
Leg right: Thigh	2032	1149	271	57	251	61	− 1
Leg		229		15			
Leg left: Thigh	1923	1068	263	51	248	57	− 2
Leg		227		11			
Total joints	16208	9223	2585	1912	2220	288	− 20
Kidneys	93						
Kidney fat	500						
Diaphragm	103						
Total carcass	16904						
Head	1405						
Feet (4)	703						
Cold carcass: head and feet	16905						

Tissue	Total	Muscle	Subcu-taneous fat	Fat between muscles	Bone	Tendon glands and waste	Loss
XII. Cheviot. Wether 4·5 months							
Neck	1450	745	139	309	188	71	– 2
Thorax	4075	2099	572	805	576	30	– 7
Shoulder right: Shoulder	1646	884	185	197	215	41	– 19
Arm		134		9			
Shoulder left: Shoulder	1580	870	155	188	215	28	– 19
Arm		134		9			
Loin	1698	1028	298	262	150	14	– 54
Pelvis	1725	925	383	200	220	7	– 10
Leg right: Thigh	1863	1056	210	68	233	61	– 13
Leg		236		12			
Leg left: Thigh	1815	1001	219	56	241	62	– 11
Leg		228		19			
Total joints	15852	9340	2161	2134	2038	314	– 135
Kidneys	96						
Kidney fat	622						
Diaphragm	128						
Total carcass	16698						
Head	1296						
Feet (4)	646						
Cold carcass: head and feet	16704						
XIII. Uruguay. Wether 4·5 months							
Neck	1530	646	201	377	216	74	16
Thorax	3920	1711	726	901	585	43	– 46
Shoulder right: Shoulder	1474	729	174	147	240	38	4
Arm		135		7			
Shoulder left. Shoulder	1471	705	171	159	243	46	1
Arm		139		7			
Loin	1632	822	394	223	164	18	11
Pelvis	1706	672	526	197	245	34	32
Leg right · Thigh	1892	996	229	68	264	59	22
Leg		242		12			
Leg left: Thigh	1735	908	177	55	266	62	15
Leg		240		12			
Total joints	15360	7945	2598	2165	2223	374	55
Kidneys	96						
Kidney fat	291						
Diaphragm	132						
Total carcass	15879						
Head	-						
Feet (4)	-						
Cold carcass	15910						
XIV. Southdown × Romney. Wether 4·5 months							
Neck	1818	748	295	192	192	45	43
Thorax	4655	1846	959	1154	506	29	161
Shoulder right: Shoulder	1697	745	306	243	189	34	39
Arm		132		9			
Shoulder left: Shoulder	1700	760	273	262	189	37	36
Arm		133		10			
Loin	2038	992	572	311	110	11	42
Pelvis	1662	615	506	262	198	11	70
Leg right: Thigh	1890	907	337	95	199	52	60
Leg		220		20			
Leg left: Thigh	2087	992	432	109	199	44	67
Leg		224		20			
Total joints	17547	8314	3680	2990	1782	263	518
Kidneys	120						
Kidney fat	562						
Diaphragm	95						
Total carcass	18324						
Head	-						
Feet (4)	-						
Cold carcass	18360						

APPENDIX III (*continued*)

Tissue	Total	Muscle	Subcutaneous fat	Fat between muscles	Bone	Tendon glands and waste	Loss
XV. B.L. × Iceland. Wether 4·5 months							
Neck	1472	750	128	271	216	36	71
Thorax	4067	2058	540	726	640	37	66
Shoulder right: Shoulder	1645	876	176	121	265	37	16
Arm		149		5			
Shoulder left: Shoulder	1633	857	202	119	273	32	- 6
Arm		149		7			
Loin	2118	1271	381	207	211	11	37
Pelvis	1716	860	354	208	255	4	35
Leg right: Thigh	1926	1062	195	51	266	57	29
Leg		251		15			
Leg left: Thigh	1874	1018	186	48	267	47	23
Leg		268		17			
Total joints	16451	9569	2162	1795	2393	261	271
Kidneys	90						
Kidney fat	395						
Diaphragm	11						
Total carcass	16947						
Head	1648						
Feet (4)	801						
Cold carcass: head and feet	16987						
XVI. Iceland Lamb. Wether 4·5 months							
Neck	1732	962	126	319	215	48	62
Thorax	4032	2082	490	661	612	31	156
Shoulder right · Shoulder	1559	821	109	113	268	30	58
Arm		149		11			
Shoulder left: Shoulder	1542	798	140	84	269	42	53
Arm		148		8			
Loin	1810	1110	307	186	165	13	29
Pelvis	1987	1010	395	222	258	11	91
Leg right: Thigh	1939	1010	147	53	299	69	70
Leg		265		26			
Leg left: Thigh	1907	1000	127	45	303	67	87
Leg		263		15			
Total joints	16508	9618	1841	1743	2389	311	606
Kidneys	99						
Kidney fat	782						
Diaphragm	72						
Total carcass	17461						
Head	1887						
Feet (4)	786						
Cold carcass: head and feet	17473						
XVII. Australian Southdown Merino Ewe Lamb 4·5 months							
Shoulder left: Shoulder	1923	994	278	224	227	29	21
Arm		142		8			
Leg left: Thigh	2110	1128	295	93	232	53	29
Leg		262		18			

Weights of individual bones of animals used in the investigation (g.)

Breed	B.L. × Blackfaced		B.L. × Cheviot		Cheviot		Oxford × B.L.-Chev.		Suffolk B.L.-Chev.		Southdown × B.L.-Chev.	Black-faced	Uruguay	Southdown × Romney	B.L. × Iceland	Iceland	Southdown × Merino
No.	XI	I	X	II	XII	III	VIII	IV	VII	V	VI	IX	XIII	XIV	XV	XVI	XVII
Age (months)	4½	13	4½	13	4½	13	4½	13	4½	13	4½	4½	4½	4½	4½	4½	4½
Skull	377	499	370	487	316	449	355	513	352	583	344	417	—	—	363	450	—
Lower jaw	100	153	105	140	95	132	97	145	105	193	97	98	—	—	101	97	—
Tongue bones	4	6	5	9	4	6	3	8	5	8	4	3	—	—	5	4	—
Atlas	37	43	33	47	26	42	37	60	37	58	30	33	32	31	36	37	—
Axis	41	52	39	51	35	50	44	62	41	60	33	38	41	37	41	40	—
Vertebrae:																	
(4–5) Cervical	117*	180	128	193	127	184	142	215	148	235	94*	126	143	124	139	138	—
Thoracic	234	247	228	293	194	298*	215	289	218	330*	180	192	214	172	233	201	—
Lumbar	166	184	165	208	150	206	203*	235	197	247	138	167	164	110*	211	163	—
Sacral	69	87	66	80	54	90	70	83	61*	93	52	43	66	55	52	52	—
Caudal (part)	14	23	14	27	15	27	21	22	20	20	13	15	14	10	15	8	—
Ribs (right)	166	249	192	239	157	245	185	291	176	292*	151	155	153	144	166	165	—
Ribs (left)	163	247	195	247	167	247*	186	296	180	292*	150	158	151	145	171	166	—
Sternum	66	105	78	89	58	101	78	107	68	102	61	57	67	45	70	80	—
Pelvis	177	229	181	218	151	235	196	255	179	285	144	140	165	133	188	198	—
Fore-limbs:																	
Right scapula	59	92	67	90	55	90	70	106	64	111	54	63	62	51	68	70	—
,, humerus	92	118	98	129	83	119	107	147	105	136	78	83	90	74	100	102	—
,, radius-ulna	68	94	75	98	64	96	82	125	82	114	57	66	72	53	81	81	—
,, carpals	15	15	17	21	13	18	17	23	17	20	13	13	16	11	16	15	—
,, fore-cannons	38·7	47·7	43	54·7	35·8	49·1	49	62·0	42	63	34	37	—	—	42	45	—
,, sessamoids 2	2·9	2·6	2·2	3·6	2·1	2·7	3	3·5	2	4	2	2·5	—	—	3	3	—
,, pasterns 2	14·6	17·6	15·4	19·7	12·9	18·7	18	23·1	17	23	11	13	—	—	16	17	—
,, coronets 2	6·8	7·5	7·2	9·2	6·2	8·5	8	9·9	8	10	6	6·1	—	—	8	7·8	—
,, naviculars 2	4·4	2·0	1·3	2·1	1·4	1·9	2	2·2	2	2	1	1·2	—	—	1·5	1·7	—
,, pedal bones 2	4·5	7·6	4·7	8·1	4·5	6·5	6	9·2	4	8	4	4·3	—	—	6	5·6	—

* Not usual number of bones. See Table 73.

APPENDIX IV (continued)

Breed	B.L. × Blackfaced	B.L. Blackfaced	B.L. × Cheviot	B.L. × Cheviot	Cheviot	Cheviot	Oxford × B.L.-Chev.	Oxford × B.L.-Chev.	Suffolk × B.L.-Chev.	Suffolk × B.L.-Chev.	Southdown × B.L.-Chev.	Blackfaced	Uruguay	Southdown × Romney	B.L. × Iceland	Iceland	Southdown × Merino
No.	XI	I	X	II	XII	III	VIII	IV	VII	V	VI	IX	XIII	XIV	XV	XVI	XVII
Age (months)	4½	13	4½	13	4½	13	4½	13	4½	13	4½	4½	4½	4½	4½	4½	4½
Fore-limbs (continued):																	
Left scapula	60	94	66	89	54	91	75	105	59	111	53	54	63	49	70	71	60
,, humerus	93	116	96	128	84	119	105	148	100	134	81	80	91	73	105	102	89
,, radius-ulna	63	96	73	99	65	95	85	123	74	111	57	63	72	54	82	81	66
,, carpals	15	16	17	22	12	18	18	24	16	20	13	12	17	13	16	15	12
,, fore-cannons	39·2	47·6	43·2	51·5	36·2	48·9	49	39·8	43	63	35	38·6	—	—	42	45	—
,, sessamoids 2	2·6	2·6	2·7	3·3	2·4	2·8	3	3·3	3	4	2·5	2·9	—	—	3	2·8	—
,, pasterns 2	14·4	17·5	15·9	19·0	13·3	18·6	18	22·2	17	25	13	13·3	—	—	16	16·1	—
,, coronets 2	6·7	7·7	7·4	8·9	6·3	8·3	8	10·0	8	10	6	6·6	—	—	8	7·8	—
,, naviculars 2	1·5	1·9	1·4	1·9	1·3	2·0	2	2·1	2	2	1·5	1·5	—	—	1·5	1·7	—
,, pedal bones 2	5·2	7·3	5·4	7·7	4·6	6·6	6	8·2	6	9	5	4·8	—	—	6	5·3	—
Hind-limbs:																	
Right femur	117	137	124	156	109	150	140	180	136	167	108	102	121	92	127	139	104
,, patella	6	7	6	9	5	8	6	12	7	9	6	6	6	4	7	7	5
,, tibia-fibula	93	120	100	130	85	129	114	154	107	152	86	88	103	76	99	115	92
,, calcaneus	15	17	15	19	14	19	18	22	17	22	13	12	15	11	15	16	13
,, astragalus	11	12	12	15	11	14	15	18	14	16	11	10	13	10	9	12	10
,, other tarsals	9	11	10	13	9	12	12	14	11	14	9	9	12	6	9	10	8
,, hind-cannon	41·3	50	44·1	53	35·7	50·2	51	60	46	63	36	38·5	7*	—	43	48	—
,, sessamoids 2	2·2	2·5	2·4	2·9	1·9	2·6	3	3·0	3	3	2	2·2	—	—	3	2·7	—
,, pasterns 2	13·2	15·1	13·8	16·6	11·3	17·5	15	19·0	15	19	12	12·1	—	—	15	14·5	—
,, coronets 2	6·1	6·8	6·4	7·5	5·3	7·7	7	8·5	5	7	6	5·7	—	—	7	6·7	—
,, naviculars 2	1·2	1·5	1·2	1·6	0·7	1·5	1	1·6	1	1	1	1	—	—	1	1·3	—
,, pedal bones 2	4·3	7·0	4·3	7·2	3·5	5·9	6	6·9	6	7	5	4·8	—	—	5	4·4	—
Left femur	117	140	123	158	117	155	142	181	136	170	105	105	119	93	125	139	—
,, patella	6	7	6	9	6	8	8	11	7	9	6	6	6	4	5	8	—
,, tibia-fibula	91	122	100	134	85	133	115	155	113	152	83	88	103	75	100	116	—
,, calcaneus	14	17	15	19	13	20	18	21	16	22	12	12	15	11	16	18	—
,, astragalus	11	12	12	15	11	14	15	18	13	16	11	10	13	10	10	12	—
,, other tarsals	9	10	10	12	9	11	11	14	10	14	9	9	10	6	11	10	—
,, hind-cannon	41·6	50	44	53·7	35·6	50	52	60	45	64	36	37·5	—	—	43	48	—
,, sessamoids 2	2·4	2·6	2·2	2·8	1·9	3·0	3	2·9	3	3	2	2·2	—	—	3	2·7	—
,, pasterns 2	13·5	15	14·1	16·7	11·2	17·2	15	19·4	15	20	11	11·8	—	—	15	14·4	—
,, coronets 2	6·2	6·4	6·4	7·6	5·4	7·1	12	8·5	7	8	5	5·5	—	—	7	6·7	—
,, naviculars 2	1·2	1·7	1·1	1·6	1·1	1·5	5	1·6	1	1	1	0·9	—	—	1	1·3	—
,, pedal bones 2	4·6	6·0	4·7	7·1	3·5	5·7	5	7·0	5	8	4	4·7	—	—	5	4·0	—

* Not usual number of bones. See Table 73.

APPENDIX V

Actual weights of different parts of the head of sheep used in the dissection

No. of sheep	XI	I	X	II	XII	III	VIII	IV	VII	V	VI	IX	XV	XVI
Breed	B.L. × Blackfaced		B.L. × Chev.		Cheviot		Oxford B.L.-Chev.		Suffolk B.L.-Chev.		Southdown × B.L. Chev.	Black-faced	B.L. × Iceland	Iceland
Age (months)	13	13	4½	13	4½	13	4½	13	4½	13	4½	4½	4½	4½
Ears	44	62	49	81	52	91	98	87	76	105	64	30	44	39
Skin	148	160	165	218	116	192	216	270	156	251	170	180	200	277
Tongue	65	106	72	118	74	105	70	94	95	97	63	63	65	112
Eyes	21	27	21	25	19	29	21	28	20	28	20	19	20	23
Horns	—	100	—	—	3	—	—	—	—	—	—	87	17	153
Glands	25	64	36	51	28	114	24	50	38	85	36	19	53	15
Muscle	319	340	323	404	302	371	353	372	342	336	359	314	304	413
Fat between and sub-cutaneous muscle	71	248	77	217	82	165	104	165	103	195	68	90	187	78
Tendon, etc.	98	96	123	104	91	136	130	157	131	233	96	141	99	82
Brain	95	104	107	113	92	104	103	125	97	103	92	110	105	94
Tongue bones	4	6	5	9	4	6	3	8	3	8	4	3	5	4
Lower jaw	100	153	105	140	95	132	97	145	105	193	97	98	101	97
Skull	377	499	370	487	316	449	355	513	352	583	344	417	363	450
Total (all parts)	1367	1965	1453	1967	1276	1894	1574	2014	1520	2217	1413	1571	1563	1837
Loss	38	70	42	66	20	62	30	55	40	73	64	31	85	50
Total head	1405	2035	1495	2033	1296	1956	1604	2069	1560	2290	1477	1602	1648	1887

Average measurements of wether lambs and hoggets, grouped

Breed and no of individuals	Av. wt. dressed carcass lb.	F	G	H	I	K	L	N	R	T	Th	A
Lambs· Weight class 25–32 lb.												
Iceland	30·50	272·00	210·0	116·0	382·5	610·0	555·0	130·0	173·0	199·00	266·5	54·00
No.	2	2	2	2	2	2	2	2	2	2	2	2
Lambs· Weight class 33–40 lb.												
Iceland	37·00	271·00	224·8	120·8	421·0	618·0	578·0	153·0	179·8	207·80	274·6	55 80
No.	5	5	5	5	5	5	5	5	5	5	5	5
B.L. × Iceland	37 25	271·00	223·8	119·8	412·5	661·2	602·5	155·0	186·0	209·00	271·8	56·75
No.	4	4	4	4	4	4	4	4	4	4	4	4
Blackfaced	36·78	239·55	219·1	122·4	406·1	605·9	562·0	157·2	161·9	183·89	248·9	51·22
No.	9	9	9	9	9	9	9	9	9	9	9	9
B.L. Blackfaced	38 13	255·07	218·6	126·5	419·3	632·0	586 7	156·0	169·2	193·33	257·3	52·67
No.	15	15	15	15	15	15	15	15	15	15	14	15
Southdown × B L ·Chev	37·96	238 39	223 7	126·3	422·0	600·2	554·6	135·6	162·7	185·70	250·0	54·04
No	23	23	23	23	23	23	23	23	23	23	23	23
Oxford × B.L.·Chev	39 75	273·00	225·0	133 5	445·0	640·0	595 5	157·5	176 8	204·75	262·5	53 25
No.	4	4	4	4	4	4	4	4	4	4	4	4
Lambs: Weight class 41–48 lb.												
Iceland	42 66	284 30	228·3	122 7	425	660	611·7	143 3	186·7	219 00	277·0	53 33
No.	3	3	3	3	3	3	3	3	3	3	3	3
B.L. · Iceland	44·60	275·00	231 4	126·0	426	697	630·0	151·0	186·0	217 80	280 8	58 60
No	5	5	5	5	5	5	5	5	5	5	5	5
B.L Blackfaced	43 25	258·00	226·9	134·4	444	657	608·8	162·0	176 1	197·62	264·4	54 25
No.	8	8	8	8	8	8	8	8	8	8	8	8
B.L. · Chev.	44·00	258·30	225 0	124 8	435	640	598 8	145·0	174 2	203·00	260·0	58 00
No.	4	4	4	4	4	4	4	4	4	4	4	4
Southdown × B.L.·Chev.	43·67	243 67	237·1	137·5	449	626	577·1	123 8	164·8	190·25	260 0	55·75
No.	12	12	12	12	12	12	12	12	12	12	12	12
Oxford × B.L.·Chev.	45 30	277·35	235·0	138·5	456	659	608·2	163·2	183 2	208·05	275·0	56·65
No.	20	20	20	20	20	20	20	20	20	20	18	20
Suffolk × B.L.·Chev	44·77	264 11	236·7	138·9	453	664	616·5	162 2	178 7	203·78	276·0	58·22
No.	9	9	9	9	9	9	9	9	9	9	9	9
Lambs· Weight class 49–56 lb.												
B.L. × Chev.	50·12	270 00	238·8	131·9	459	664	618·8	155·0	183·6	208·88	270·0	55·62
No.	8	8	8	8	8	8	8	8	8	8	8	8
Southdown × B.L.·Chev.	49·50	238 50	240·0	137·5	460	652	597·5	107·5	165·0	194·50	265·0	57·50
No.	2	2	2	2	2	2	2	2	2	2	2	2
Oxford × B.L.·Chev	52·81	282 62	241·9	143·8	477	701	646·6	165·6	188·9	214 12	280·0	59·31
No.	16	16	16	16	16	16	16	16	16	16	15	16
Suffolk × B.L ·Chev.	52 78	267·28	240·8	140·8	471	687	637·8	163·8	186·1	212·33	278·3	58·39
No.	18	18	18	18	18	18	18	18	18	18	18	18
Lambs: Weight class 57–64 lb.												
B L. Chev.	57·33	262 67	246·6	138·3	480	660	633·3	150·0	186·0	208·00	275·0	62·33
No	3	3	3	3	3	3	3	3	3	3	3	3
Oxford × B.L.·Chev.	57·75	291 25	248·8	146·2	485	711	648·8	170·0	200·5	227·50	283·8	60·50
No.	4	4	4	4	4	4	4	4	4	4	4	4
Suffolk × B.L.·Chev.	59 60	265 40	253·0	148·0	491	717	657·0	160·0	183·4	211·00	279·0	58·60
No.	5	5	5	5	5	5	5	5	5	5	5	5

in weight classes of 8 lb. All linear measurements in millimetres

								Left fore-cannon bone			
B	C	D	J	X	Y	S	Length	Min. circ.	Wt. g.	Wt./Length ×100	of eye muscle
21·50	2·50	1·50	6·50	7·50	1·50	23·5	118·50	44·00	36·50	30·85	11·5
2	2	2	2	2	2	2	2	2	2	2	2
23·40	2·60	1·20	8·00	10·00	2·50	25·2	122·00	45·60	41·40	33·92	11
5	5	5	5	5	5	5	5	5	5	5	5
25·25	3·25	2·25	7·75	9·50	3·00	25·0	122·50	47·00	45·75	37·32	10·25
4	4	4	4	4	4	4	4	4	4	4	4
28·11	2·67	3·00	8·67	11·78	3·78	24·6	109·11	43·33	35·44	32·52	10·8
9	9	9	9	9	9	9	9	9	9	9	9
27·80	4·53	3·73	11·60	10·93	4·87	24·2	113·93	43·71	37·71	33·09	10·3
15	15	15	15	15	15	15	14	14	14	14	6
30·43	3·30	4·97	10·70	11·96	4·09	22·7	107·78	45·00	35·43	32·76	9
23	23	23	23	23	23	23	23	23	23	23	11
26·50	2·50	2·75	8·00	9·25	3·00	23·2	119·50	47·50	46·75	39·10	·
4	4	4	4	4	4	4	4	4	4	4	·
23·67	3·00	2·00	10·00	12·30	3·33	27·0	130·67	46·67	45·33	34·70	10
3	3	3	3	3	3	3	3	3	3	3	3
27·40	5·20	4·20	13·00	11·60	3·60	25·4	126·80	48·20	49·00	38·64	10·4
5	5	5	5	5	5	5	5	5	5	5	5
30·12	5·38	4·50	12·00	11·38	4·88	24·0	116·12	44·50	40·38	34·75	10·2
8	8	8	8	8	8	8	8	8	8	8	4
28·00	3·25	2·50	9·50	11·00	3·50	24·5	122·75	49·25	48·25	39·28	10
4	4	4	4	4	4	4	4	4	4	4	4
33·33	3·83	5·67	13·00	11·58	6·08	22·8	112·42	47·58	41·08	36·47	—
12	12	12	12	12	12	12	12	12	12	12	
27·35	3·35	3·65	10·60	10·95	4·55	24·8	124·15	48·50	50·35	40·55	9·1
20	20	20	20	20	20	20	20	20	20	20	8
31·11	3·22	3·44	10·55	10·11	5·11	25·4	121·88	48·88	49·88	40·80	·
9	9	9	9	9	9	9	8	8	8	8	
29·62	4·25	3·75	13·00	13·25	4·00	25·1	123·00	48·88	49·00	40·42	10·6
8	8	8	8	8	8	·8	8	8	8	8	7
34·50	7·00	8·50	15·50	14·00	7·00	23·0	108·00	48·50	40·40	37·50	--
2	2	2	2	2	2	2	2	2	2	2	--
27·69	4·31	4·38	11·81	10·94	4·91	25·5	127·25	50·69	56·00	43·99	8·5
16	16	16	16	16	16	16	16	16	16	16	8
31·50	4·83	5·33	13·89	13·28	5·33	24·9	121·28	50·22	51·83	42·74	10·4
18	18	18	18	18	18	18	18	18	18	18	5
30·67	7·33	10·00	18·33	13·00	6·00	27·3	121·67	50·33	52·66	43·20	10·5
3	3	3	3	3	3	3	3	3	3	3	2
28·75	5·50	5·75	13·75	13·50	4·25	26·8	131·75	51·50	59·25	41·88	9·5
4	4	4	4	4	4	4	4	4	4	4	4
35·40	6·40	7·00	20·60	13·40	10·80	25·4	125·20	50·80	57·00	45·56	10
5	5	5	5	5	5	5	5	5	5	5	3

Breed and no. of individuals	Av. wt. dressed carcass lb.	F	G	H	I	K	L	M	R	T	A
Hoggets: Weight class 33–40 lb.											
B.L. × Blackfaced	39	272·50	215·0	132·5	428	640	570·0	—	170·0	209·50	55·50
No.	2	2	2	2	2	2	2	—	2	2	2
Cheviot	37·18	246·54	229·1	126·8	422	618	557·3	112·8	168·2	194·18	56·27
No.	11	11	11	11	11	11	11	11	11	11	11
Hoggets: Weight class 41–48 lb.											
B.L. × Blackfaced	45·50	264·94	234·6	131·2	439	666	595·6	120·4	177·0	208·31	56·19
No.	16	16	16	16	16	16	16	10	16	16	16
Cheviot	44·14	244·10	232·4	129·0	439	626	571·7	113·4	171·4	199·05	56·81
No.	21	21	21	21	21	21	21	20	21	21	21
B.L.-Chev.	46 00	265·50	238·3	134·1	444	670	609·1	123·0	178·0	206·00	54·17
No.	6	6	6	6	6	6	6	3	6	6	6
Southdown × B.L.-Chev.	41·00	266 50	240·0	132·5	425	625	550	—	161	197·5	51 50
No.	2	2	2	2	2	2	2	—	2	2	2
Oxford × B.L.-Chev.	45·00	298·00	230·0	135 0	440	710	640·0	138·0	200·0	235·00	59·00
No.	1	1	1	1	1	1	1	1	1	1	1
Suffolk × B.L.-Chev.	45·50	279·50	235·0	130·0	442	662	607·5	128·0	178·0	217·00	55·00
No.	2	2	2	2	2	2	2	2	2	2	2
Hoggets: weight class 49–56 lb.											
B.L. × Blackfaced	52·85	269 04	244·2	138 1	463	684	614·6	126·8	180·6	213·73	57·15
No.	26	26	26	26	26	26	26	12	26	26	26
Cheviot	53·00	259·33	241·7	135·0	468	652	605·0	121·7	178·7	209·00	57·67
No.	3	3	3	3	3	3	3	3	3	3	3
B.L.-Chev.	53·87	273·66	249·7	142·0	471	695	622·0	129·1	187·6	217·73	58·20
No.	15	15	15	15	15	15	15	13	15	15	15
Oxford × B.L.-Chev.	53·80	284 00	248·0	144·0	471	706	646·0	132·8	193·4	222·60	60·80
No.	5	5	5	5	5	5	5	5	5	5	5
Suffolk × B.L.-Chev.	52·86	276 28	254·3	141·4	482	695	605·0	128·3	183·6	216·28	59·00
No.	7	7	7	7	7	7	7	3	7	7	7
Suffolk	53 37	288·88	264·4	134·1	464	705	625·6	128·4	193·5	227·88	63·38
No.	8	8	8	8	8	8	8	8	8	8	8
Hoggets: Weight class 57–64 lb											
B.L. × Blackfaced	59·27	274 81	251·4	141·3	477	704	636·0	127·1	186·0	219·46	57 85
No.	26	26	26	26	26	26	26	12	26	26	26
Cheviot	59·86	266 71	248·6	140·0	491	686	622·9	125·8	182·4	214·00	65 14
No.	7	7	7	7	7	7	7	6	7	7	7
B.L. × Chev.	60 25	280 00	253·5	146·2	489	718	645·5	132·5	192·4	224·12	59·75
No.	69	69	69	69	69	69	69	63	69	69	69
B.L. × Chev.	60 85	283 85	252·7	148·1	490	719	653·0	131·5	192·0	225·80	60·15
No.	20	20	20	20	20	20	20	13	20	20	20
Suffolk × B.L.-Chev.	60 44	277·44	263·6	147·2	502	724	639·2	—	185·6	219·72	60·72
No.	25	25	25	25	25	25	25	—	25	25	25
Suffolk	60 61	286·31	270·8	140·4	478	727	648·8	129·6	200·2	231·54	62·92
No.	13	13	13	13	13	13	13	13	13	13	13
Hoggets· Weight class 65–72 lb.											
B.L. × Blackfaced	70·50	283·75	263·8	152·5	510	754	678·8	132·0	196 2	230·25	59·30
No.	4	4	4	4	4	4	4	3	4	4	4
Cheviot	67·00	274·50	267·5	147·5	518	715	650·0	138·0	186·0	223·50	64·00
No.	2	2	2	2	2	2	2	1	2	2	2
B.L. × Chev.	68·00	282·13	264·1	150·4	502	734	660·0	134·1	195·3	226·52	60·65
No.	23	23	23	23	23	23	23	17	23	23	23
Oxford × B.L.-Chev.	68·08	286·39	263·3	152·4	508	741	664·8	133·4	194·6	228·13	60·43
No.	23	23	23	23	23	23	23	15	23	23	23
Suffolk × B.L.-Chev.	67 80	280·47	269·0	153·0	508	738	648·7	133·6	189·6	222·87	61·20
No.	15	15	15	15	15	15	15	5	15	15	15
Suffolk	69·11	288·22	277 2	145·6	497	738	658·3	130·0	204·8	234·28	65·17
No.	18	18	18	18	18	18	18	18	18	18	18
Hoggets. Weight class 73–80 lb.											
B.L. × Chev.	78·33	286·00	278·5	151·7	522	174	660·0	137·0	198·3	230·00	60·00
No.	3	3	3	3	3	3	3	1	3	3	3
Oxford × B.L.-Chev.	77·75	279·75	273·7	160·0	528	748	672·5	135·7	191·2	229·75	62·25
No.	4	4,	4	4	4	4	4	4	4	4	4
Suffolk × B.L.-Chev.	77·25	294·75	272·5	151·2	545	754	676·2	138·5	202·2	231·50	62·75
No.	4	4	4	4	4	4	4	4	4	4	4
Suffolk	76·69	293·15	280·4	148·8	507	754	671·2	130·2	210·7	238·08	64·54
No.	13	13	13	13	13	13	13	13	13	13	13
Hoggets· Weight class 81–88 lb.											
Oxford × B.L.-Chev.	82·00	283·50	272·5	165·0	540	745	685·0	137·0	201·0	232·00	64·00
No.	2	2	2	2	2	2	2	2	2	2	2
Suffolk	84·25	289·75	283·8	153·8	528	771	678·7	132·5	209·8	239·25	67·00
No.	4	4	4	4	4	4	4	4	4	4	4

							Left fore-cannon			
B	C	D	J	X	Y	S	Length	Min. circ.	Wt.	$\frac{\text{Wt.}}{\text{Length}} \times 100$
28·50	1·50	2·00	8·00	5·50	6·00	23·5	119·50	46·50	39·90	33·40
2	2	2	2	2	2	2	2	2	2	2
25·27	1·91	3·01	7·45	8·54	4·00	21·1	112·09	45·82	36·36	32·16
11	11	11	11	11	11	11	11	11	11	11
26·12	4·94	4·38	13·31	9·25	8·19	25·4	119·87	48·07	41·30	34·44
16	16	16	16	16	16	16	15	15	15	15
28·00	4·19	5·00	12·95	10·33	8·28	21·6	113·25	47·75	37·72	33 35
21	21	21	21	21	21	21	20	20	20	20
27·00	4·83	4·83	14·00	9·33	7·17	25·5	122·25	46 50	39·40	32·23
6	6	6	6	6	6	6	4	4	4	4
27·50	5·00	7·00	11·50	9·50	10·00	23·5	116·00	44·50	35·35	30 50
2	2	2	2	2	2	2	2	2	2	2
24·00	2·00	3·00	9·00	6·00	3·00	30·0	139·00	46·00	46·30	33·31
1	1	1	1	1	1	1	1	1	1	1
28·00	4·50	4·00	13·50	9·00	8·50	23·5	125·50	45·50	41·00	32 70
2	2	2	2	2	2	2	2	2	2	2
29·42	6·50	6·38	17·15	10·08	10·50	26·9	123·46	48·46	43·59	35·32
26	26	26	26	26	26	26	24	24	22	22
31·67	6·00	8·00	15·00	11·67	11 00	24·0	119·67	50·33	43·27	36·10
3	3	3	3	3	3	3	3	3	3	3
28·67	5·20	5·40	15·67	9·33	9·00	25·4	128·23	49 92	46·70	36 36
15	15	15	15	15	15	15	13	13	13	13
27·80	3·40	4·40	11·20	9·40	6·60	25·6	131·80	51 00	52·44	39 76
5	5	5	5	5	5	5	5	5	5	5
32·86	3·86	6·14	12·57	10·14	6·57	25·0	126·60	50·40	48 86	38 60
7	7	7	7	7	7	7	5	5	5	5
31·00	3·75	6·12	12·50	10·12	7·38	25·8	126·83	47·67	47·65	37 47
8	8	8	8	8	· 8	8	6	6	6	6
30 31	7·85	7·38	20·92	11·35	12 04	28·0	125·00	50 88	47 80	38 23
26	26	26	26	26	26	26	18	18	18	18
29 71	5·14	5·43	14·57	12·57	8·28	27·1	124·83	51 33	49 57	39 68
7	7	7	7	7	7	7	6	6	6	6
30·49	5 90	7·10	17·39	11·01	9·83	26·5	131·54	52 02	52 15	39·59
69	69	69	69	69	69	69	66	66	65	65
28·90	5 50	5 80	17·25	11·45	10 30	26·4	133·50	54·10	55·66	41 63
20	20	20	20	20	20	20	20	20	20	20
32 28	5·24	6 88	17 20	11·16	11·48	26·1	124·16	52 39	51 52	41·46
25	25	25	25	25	25	25	18	18	18	18
32·15	6·31	9·77	17·62	12 31	9 38	23·7	130·00	49 25	52·95	40 74
13	13	13	13	13	13	13	8	8	8	8
33 50	12 00	10·25	25·75	13·75	10·50	32·5	130·00	53·75	56·50	43 55
4	4	4	4	4	4	4	4	4	4	4
35·00	6·00	13·50	19·00	14·00	10·50	23·5	138·00	50·00	54·00	39·10
2	2	2	2	2	2	2	1	1	1	1
31·56	7·96	9·61	22·26	12·30	12·70	27·1	133·24	53·24	56·14	42·14
23	23	23	23	23	23	23	21	21	21	21
30 61	7·87	8·96	22·96	13·04	13·22	27·7	133·04	53 36	55 63	41·74
23	23	23	23	23	23	23	22	22	21	21
33·27	8·67	9·40	23·53	13·87	12·60	26 4	128·93	52·21	54·56	42·29
15	15	15	15	15	15	15	14	14	14	14
33·06	6·56	10·44	19·61	12·67	11·00	26·8	129·33	50·92	53·95	41·72
18	18	18	18	18	18	18	13	13	13	13
34·33	11·33	10 67	29·67	13 00	19·33	31·0	133·00	55·50	59·10	44·40
3	3	3	3	3	3	3	2	2	2	2
31·25	10·05	10·25	27·25	13·00	16·25	29·2	136·25	59 00	64·35	47·10
4	4	4	4	4	4	4	4	4	4	4
35·00	6·00	9·25	27·25	14·00	12·25	28·5	137·00	53·75	61·33	44·78
4	4	4	4	4	4	4	4	4	4	4
33·23	7·85	12·62	21·46	12·38	14·15	26·7	131·00	52·33	57·69	43·94
13	13	13	13	13	13	13	12	12	12	12
36·50	8·00	8·00	26·00	12·00	14·00	29·0	138·00	57·50	64·85	47·05
2	2	2	2	2	2	2	2	2	2	2
34·50	12·23	15·50	28·75	15·25	15·75	29·2	129·3	53·70	55·52	43·17
4	4	4	4	4	4	4	3	3	3	3

Average carcass weights, measurements and number o

Breed	Sex	Average carcass wt. (lb)	F	G	H	I	K	L	N	R	T	Th
Weight class 25–32 lb.												
Iceland	Rams	29·10	266·7	213·0	110·0	384·0	599·0	553·0	124·0	170·0	196·4	260·0
	No.	14	14	14	14	14	14	14	14	14	14	14
	Ewes	29·33	263·0	213·3	112·7	363·3	598·3	556·7	125·0	170·3	196·3	254·0
	No.	3	3	3	3	3	3	3	3	3	3	3
B.L. × Iceland	Rams	30·12	270·6	215·4	110·8	391·2	625·0	588·8	136·9	175·5	200·4	259·5
	No.	8	8	8	8	8	8	8	8	8	8	8
	Ewes	29·40	259·8	218·2	116·0	396·0	627·0	566·0	139·0	166·0	190·6	253·2
	No.	5	5	5	5	5	5	5	5	5	5	5
Weight class 33–40 lb.												
Iceland	Rams	35·51	275·0	220·0	115·0	402·0	643·0	587·0	133·0	180·0	207·0	273·0
	No.	13	13	13	13	13	13	13	13	13	13	13
B.L. × Blackfaced	Ewes	37·25	257·0	221·2	118·8	417·5	621·2	582·5	247·5	167·2	186·0	178·8
	No.	4	4	4	4	4	4	4	4	4	4	4
B.L. × Iceland	Rams	37·50	262·8	229·2	124·0	417·5	675·0	597·5	128·8	178·0	202·2	270·8
	No.	4	4	4	4	4	4	4	4	4	4	4
	Ewes	37·28	271·4	223·6	117·0	416·4	659·3	607·1	138·6	180·1	206·6	208·3
	No.	7	7	7	7	7	7	7	7	7	7	7
Weight class 41–48 lb.												
Iceland	Rams	43·00	285·0	229·0	120·0	429·0	662·0	611·0	138·6	184·3	216·3	283·0
	No.	7	7	7	7	7	7	7	7	7	7	7
B.L. × Iceland	Rams	48·00	273·0	243·0	135·0	460·0	710·0	635·0	120·0	188·0	210·0	257·0
	No.	1	1	1	1	1	1	1	1	1	1	1
	Ewes	42·75	273·5	228·8	124·0	431·0	708·8	621·2	140·0	186·0	212·8	276·2
	No.	4	4	4	4	4	4	4	4	4	4	4
Oxford × B.L.-Chev.	Ewes	46·00	271·2	227·5	136·2	447·5	675·0	622·5	173·0	185·2	207·2	265·0
	No.	4	4	4	4	4	4	4	4	4	4	4
Weight class 49–56 lb.												
B.L. × Cheviot	Ewes	51·25	281·0	240·0	136·2	462·5	697·5	622·5	136·2	193·2	217·5	272·5
	No.	4	4	4	4	4	4	4	4	4	4	4

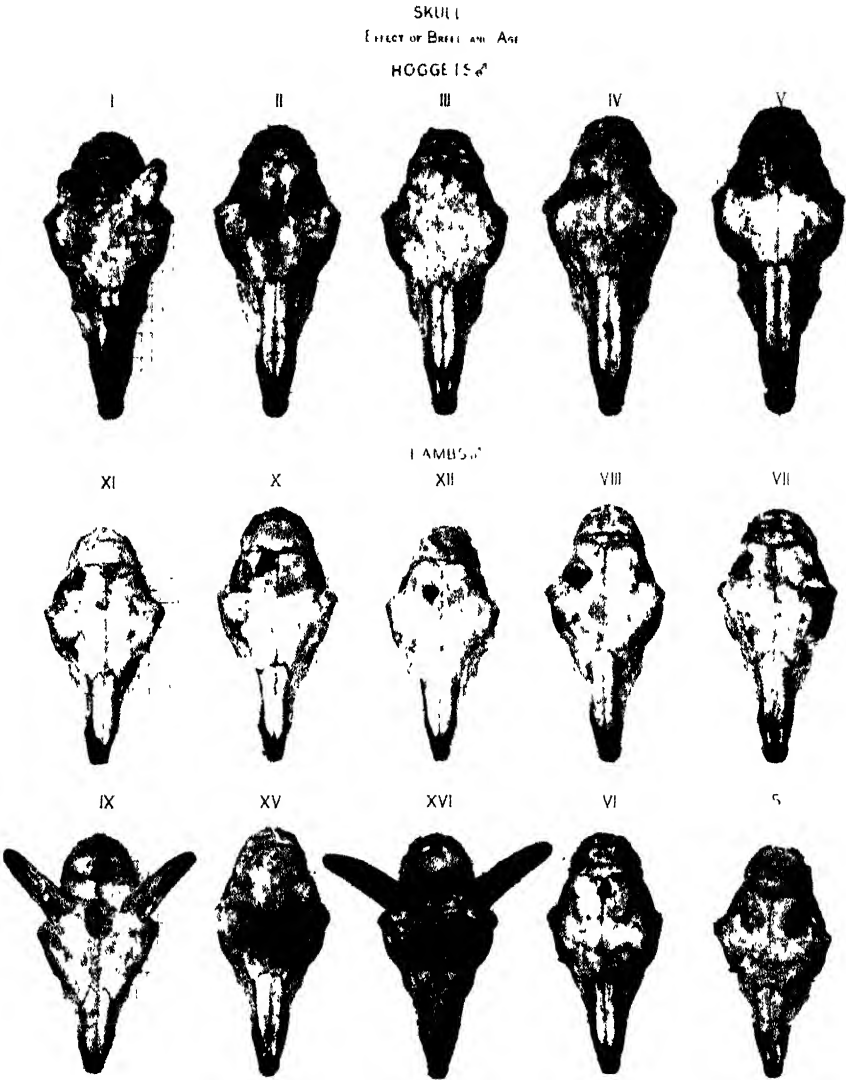*individuals of non-castrated male and female lambs*

| A | B | C | D | J | X | Y | S | Cannon-bone | | | | Colour of muscle |
								Length	Min. circ.	Wt.	$\dfrac{\text{Wt.}}{\text{Length}} \times 100$	
50·36	20·36	1·78	1·14	5·50	9·3	2·1	23·6	116·5	42·0	35·6	30·6	10·9
14	14	14	14	14	14	14	14	14	14	14	14	14
50·67	24·00	2·67	1·67	8·00	9·7	2·33	22·0	118·0	41·0	34·0	28·8	12·0
3	3	3	3	3	3	3	3	3	3	3	3	3
53·38	22·12	1·88	1·12	4·62	7·4	1·7	24·1	118·5	44·5	41·7	35·2	10·7
8	8	8	8	8	8	8	8	8	8	8	8	8
51·80	23·20	2·40	1·40	7·20	8·6	2·6	23·2	112·0	40·2	33·0	29·4	10·8
5	5	5	5	5	5	5	5	5	5	5	5	5
52·80	22·22	1·61	1·47	6·38	9·7	3·5	23·2	121·8	43·9	40·0	33·0	10·9
13	13	13	13	13	13	13	13	13	13	13	13	13
51·25	28·00	3·00	2·75	12·75	12·5	5·0	22·8	109·5	41·5	33·7	33·4	9·5
4	4	4	4	4	4	4	4	4	4	4	4	4
54·50	25·00	4·25	1·75	10·50	9·0	3·7	25·5	120·8	44·5	41·2	34·2	11·0
4	4	4	4	4	4	4	4	4	4	4	4	4
53·30	24·71	3·14	1·71	9·43	10·4	2·6	25·3	119·6	44·7	39·9	34·7	11·7
7	7	7	7	7	7	7	7	7	7	7	7	7
55·71	26·30	3·29	2·71	10·40	10·4	3·3	26·0	126·4	47·9	46·9	37·0	9·9
7	7	7	7	7	7	7	7	7	7	7	7	7
54·00	25·00	7·00	2·00	16·00	14·0	7·0	28·0	125·0	49·0	51·0	40·8	12·0
1	1	1	1	1	1	1	1	1	1	1	1	1
55·75	27·00	5·25	4·75	13·50	12·8	4·2	26·0	123·2	44·5	43·7	34·6	10·5
4	4	4	4	4	4	4	4	4	4	4	4	4
55·50	28·00	5·25	6·50	15·50	10·5	7·2	24·0	123·0	47·2	47·0	38·2	8·5
4	4	4	4	4	4	4	4	4	4	4	4	4
57·00	29·75	6·50	7·25	13·75	14·5	4·7	24·0	126·2	49·0	50·5	39·2	10·0
4	4	4	4	4	4	4	4	4	4	4	4	4

Dates of killing the sheep measured during the investigation

	Iceland	B.L.× Iceland	Black-faced	B.L.× Black-faced	Cheviot	B.L.× Chev.	Southdown× B.L.-Chev.	Oxford× B.L.-Chev.	Suffolk× B.L.-Chev.	Suffolk
Hoggets										
1936										
21. xii –3. i. 37	—	—	—	—	—	—	—	—	—	10
1937										
4. i –17. i	—	—	—	—	—	—	—	—	—	48
18. i –31. i	—	—	—	—	—	—	—	—	—	32
1. ii –14. ii	—	—	—	—	—	56	—	91	35	—
15. ii –28. ii	—	—	—	—	—	75	—	15	13	—
1. iii –14. iii	—	—	—	7	1	26	—	9	10	—
15. iii –28. iii	—	—	—	28	38	18	7	8	29	—
29. iii –11. iv	—	—	—	4	9	44	—	8	6	—
12. iv –25. iv	—	—	—	53	2	—	6	3	11	—
26. iv – 9. v	—	—	—	1	2	5	—	8	8	—
Lambs										
5. vii –18. vii	—	—	—	7	—	—	10	8	5	—
19. vii – 1. viii	—	—	—	13	—	2	28	15	15	—
2. viii–15. viii	—	—	11	9	—	—	6	5	23	—
16. viii–29. viii	—	—	1	17	1	18	15	25	11	—
30. viii–12. ix	—	—	—	2	—	5	3	—	2	—
13. ix –26. ix	49	40	—	—	—	—	—	—	—	—

SKULL

EFFECT OF BREED AND AGE

HOGGETS ♂

I　　II　　III　　IV　　V

LAMBS ♂

XI　　X　　XII　　VIII　　VII

IX　　XV　　XVI　　VI　　S

I and XI	B L Blackfaced	IX	Blackfaced.
II and X	B L Cheviot	XV	B L Iceland.
III and XII	Cheviot.	XVI	Iceland
IV and VIII	Oxford - B L -Cheviot.	VI	Southdown B L -Cheviot
V and VII	Suffolk B L -Cheviot.	S.	Southdown.

FORE CANNON

EFFECT OF BREED AND AGE
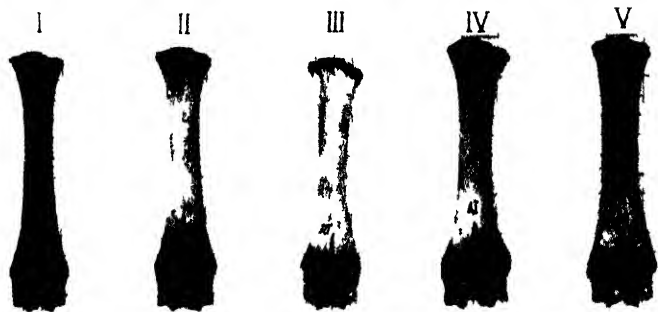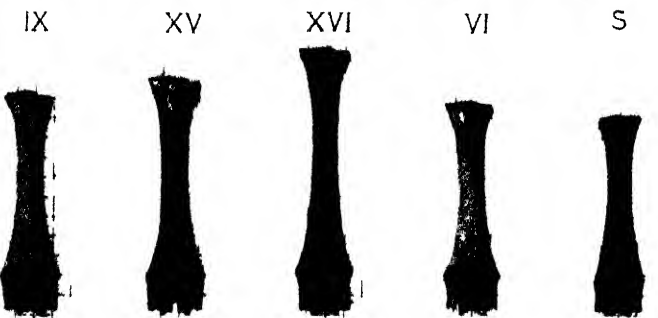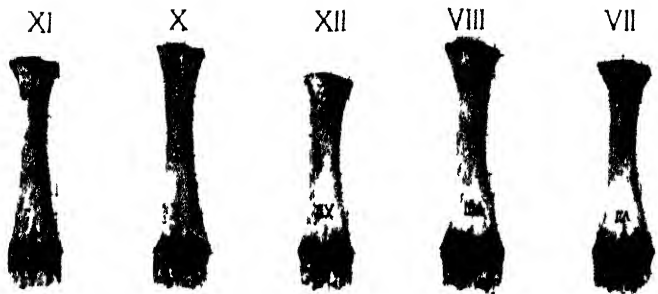
HOGGETS♂

I   II   III   IV   V

LAMBS♂

XI   X   XII   VIII   VII

IX   XV   XVI   VI   S

I and XI	B F Blackfaced	IX	Blackfaced
II and X	B F Cheviot	XV	B F Iceland
III and XII	Cheviot	XVI	Iceland
IV and VIII	Oxford B F Cheviot	VI	Southdown B F Cheviot
V and VII	Suffolk B L Cheviot	S	Southdown

HIND CANNON Effect of Breed and Age
HOGGETS♂

I   II   III   IV   V

LAMBS♂

XI   X   XII   VIII   VII

IX   XV   XVI   VI

I and XI   B L   Blackfaced.   IX.   Blackfaced.
II and X   B L   Cheviot   XV.   B.L. Iceland.
III and XII. Cheviot   XVI.   Iceland
IV and VIII   Oxford B L.-Cheviot   VI.   Southdown B.L.-Cheviot
V and VII.   Suffolk B.L.-Cheviot.

FEMUR : Effect of Breed and Age

HOGGETS ♂

LAMBS ♂

I and XI	B L Blackfaced	IX	Blackfaced.
II and X	B L Cheviot	XV	B L Iceland
III and XII	Cheviot	XVI	Iceland
IV and VIII	Oxford B L -Cheviot	VI	Southdown B L Cheviot
V and VII	Suffolk B L Cheviot	XIV	Southdown Romney
		XIII.	Uruguay

I and XI   B L   Blackfaced.   IX.   Blackfaced.
II and X   B L   Cheviot   XV.   B L   Iceland
III and XII   Cheviot.   XVI   Iceland
IV and VIII   Oxford   B L Cheviot   VI   Southdown   B L -Cheviot
V and VII.   Suffolk   B L Cheviot.   XIV.   Southdown   Romney
                                          XIII. Uruguay.

6th RIB Effect of Breed and Age

HOGGETS ♂

I   II   III   IV   V

LAMBS ♂

XI   X   XII   VIII   VII

IX   XV   XVI   VI   XIV

XIII

For description see Plate IV.

LUMBAR VERTEBRAE Effect of Breed and Age
HOGGETS ♂

I — II — III — IV — V

LAMBS ♀

XI — X — XII — VIII — VII

IX — XV — XVI — VI — XIV
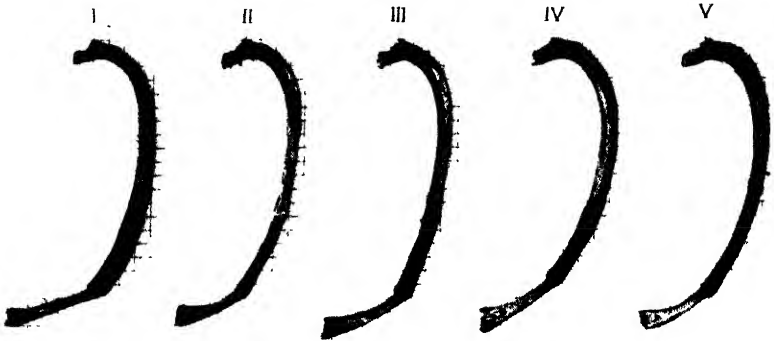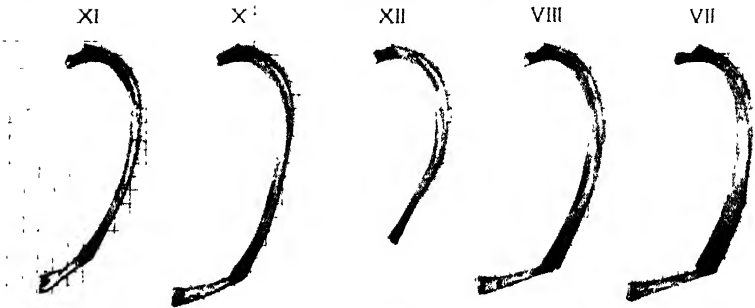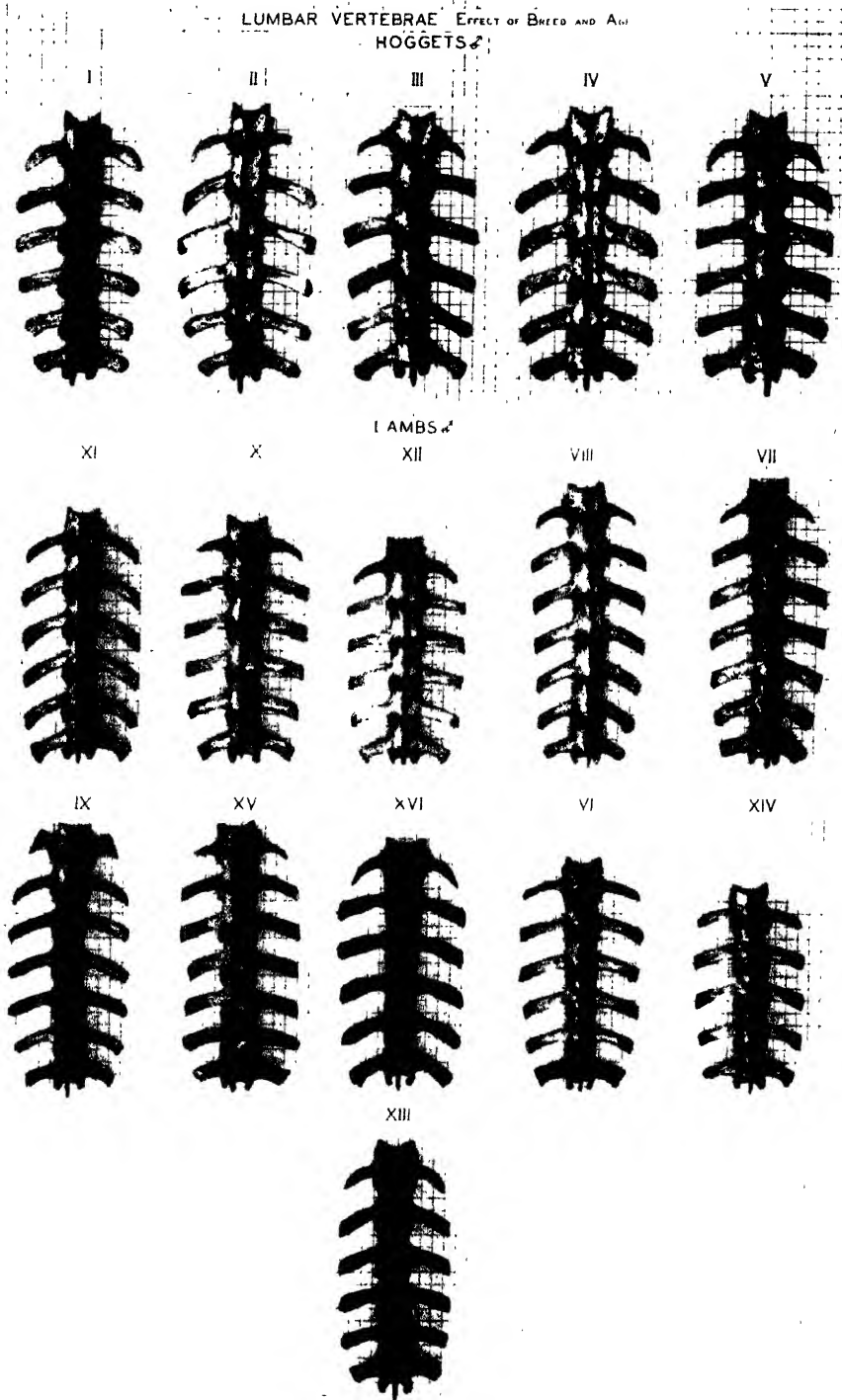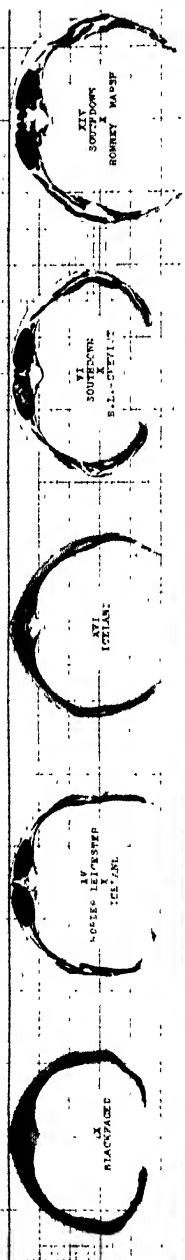
XIII
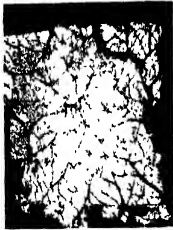
For description see Plate IV.

Hoggs, carcass weight 60 lb.
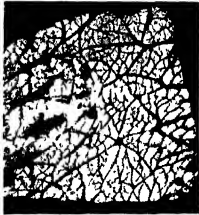
Lambs, carcass weight 40 lb.

Grain of muscle, for description see Plate VIII.

Hoggets (carcass weight (60 lb.)

Lambs (carcass weight 40 lb.)

V

IV

III

II

I

VII   B. L.×Cheviot.
Suffolk

VIII   B. L.×Cheviot.
Oxford
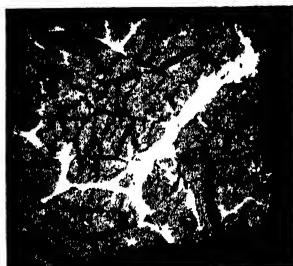
XII
Cheviot
Marbling fat.
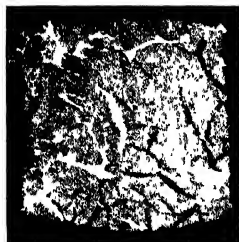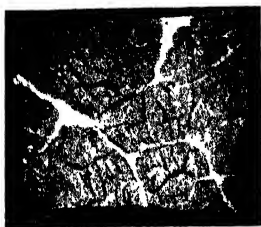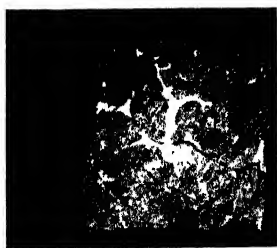
X
B.L.×Cheviot

XI
B.L.×Blackfaced
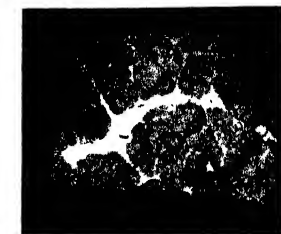
Lambs (carcass weight 40 lb.)
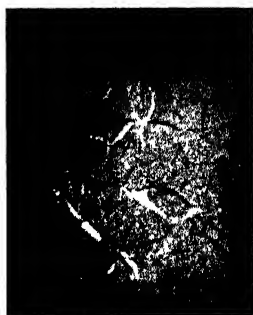
VI
Southdown × B L. × Cheviot

XIV
Southdown × Romney

IX
Blackfaced
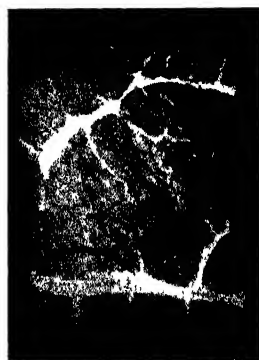
XIII
Uruguay
Marbling fat

XV
B L. × Iceland

XVI
Iceland

BODY PROPORTIONS IN SHEEP

Hoggets (carcass weight 60 lb.)

Lambs (carcass weight 40 lb.)

All to same leg length

No I. B. Leicester
    x
    Blackfaced
II B. Leicester
    x
    Cheviot
III Cheviot
IV Oxford
    x
    B L.-Cheviot
V Suffolk
    x
    B L.-Cheviot
VI Southdown
    x
    B.L.-Cheviot
VII Suffolk
    x
    B L.-Cheviot
VIII Oxford
    x
    B L.-Cheviot
IX Blackfaced
X B Leicester
    x
    Cheviot
XI B Leicester
    x
    Blackfaced
XII Cheviot
XIII Uruguay
XIV Southdown
    x
    Romney
XV B Leicester
    x
    Iceland
XVI Iceland

THE NUTRITION OF THE BACON PIG

V. THE MINIMUM LEVEL OF PROTEIN INTAKE CONSISTENT WITH QUICK GROWTH AND SATISFACTORY CARCASS QUALITY (PART II)

By H. E. WOODMAN, M.A., Ph.D., D.Sc.
and R. E. EVANS, M.Sc., Ph.D.

School of Agriculture, Cambridge

INTRODUCTION

IN the third paper of this series (Woodman *et al.* 1939) an account was given of feeding trials in which pigs subsisting on a low level of protein-food intake gave as good results, from the standpoints of growth, efficiency of food conversion and carcass quality, as pigs receiving the higher amounts of protein-rich food usually considered necessary for satisfying the protein requirements of the rapidly growing pig. The protein supplement in the feeding treatments consisted of a mixture of ex. soya bean meal, dried separated milk and feeding blood meal, this being fed in conjunction with barley meal, weatings and a small allowance of lucerne meal. The pigs on the low-protein treatment received 6% of this supplement up to 90 lb. live-weight, this being equivalent, on the basis of protein content, to $4\frac{1}{2}$% of white fish meal. The amount of the supplement was reduced to 5% at 90 lb. and again to $2\frac{1}{2}$% at 150 lb. live weight, so that in the final stage of feeding the animals were receiving the equivalent of 1·9% of white fish meal. The pigs on the standard-protein supply were given *double* these amounts of the protein supplement.

Before proceeding to a more comprehensive investigation of the problem of the protein supply of bacon pigs, it was considered desirable that the experiments already carried out should be repeated, making use this time of a totally different form of protein supplement, since the question of the biological efficiency of the protein supply may conceivably be of critical importance at the lower levels of protein feeding. In the repeat trials, therefore, the mixture of ex. soya bean meal, dried separated milk and feeding blood meal has been replaced by a single food, namely, white fish meal. The scheme of the feeding treatments is shown in Table I. It will be noted that the feeding treatment A is the low-protein treatment of the previous trial, this having been included so as to provide a link between the results of the two separate investigations.

Table I. *Scheme of feeding treatments*

	Low-protein treatment A (parts by weight)				Low-protein treatment B (parts by weight)	Standard-protein treatment C (parts by weight)
Up to 90 lb. L.W.:						
Barley meal	61		Barley meal		62	55
Weatings	31		Weatings		31	31
Lucerne meal	2		Lucerne meal		2	2
Ex. soya bean meal	3 ⎫		White fish meal		5	12
Dried separated milk	2 ⎬ 6		Minerals		1	—
Feeding blood meal	1 ⎭					
Minerals*	2					
% dig. protein in ration	10·2				10·5	14·0
90–150 lb. L.W.:						
Barley meal	70		Barley meal		71	65
Weatings	23		Weatings		23	23
Lucerne meal	2		Lucerne meal		2	2
Ex. soya bean meal	2·5 ⎫		White fish meal		4	10
Dried separated milk	1·5 ⎬ 5		Minerals		1	—
Feeding blood meal	1·0 ⎭					
Minerals	2					
% dig. protein in ration	9·5				9·5	12·6
150–200 lb. L.W.:						
Barley meal	82·5		Barley meal		82	80
Weatings	13		Weatings		13	13
Lucerne meal	2		Lucerne meal		2	2
Ex. soya bean meal	1·25 ⎫		Ex. soya bean meal†		3	5
Dried separated milk	0·75 ⎬ 2·5		Minerals		2	2
Feeding blood meal	0·50 ⎭					
Minerals	2					
% dig. protein in ration	7·9				8·0	8·6

* The minerals throughout consisted of 1 part by weight of common salt to 3 parts of ground chalk.

† Substituted for white fish meal at this stage to eliminate risk of taint.

Table II. *Average composition of feeding stuffs*

	Barley meal %	Weatings %	Lucerne meal %	Ex. soya bean meal %	Dried separated milk %	Feeding blood meal %	White fish meal %
Moisture	17·60	14·20	11·70	13·60	9·57	10·40	12·80
Crude protein	8·09	16·83	23·18	43·76	35·00	82·42	59·01
Ether extract	1·99	4·86	7·02	1·63	0·54	0·79	3·44
N-free extractives	66·68	55·52	34·22	30·15	47·37	2·61	—
Crude fibre	3·41	5·51	14 07	5·37	—	—	—
Ash	2·23	3·08	9·81	5·49	7·52	3·78	24·75
Iodine value of oil	120	127	125	110	44	61	150

Table III. *Feeding chart**

L.W. in lb.	lb. meal	L.W. in lb.	lb. meal
20	1·10	120	5·30
40	2·10	140	5·90
60	3·00	160	6·45
80	4·00	180	6·70
100	4·60	200	7·00

* Change in meal allowance shown for live-weight increments of 20 lb.; adjustments should be made for intermediate live-weights, so that the meal supply may be altered week by week in accordance with the results of the weekly weighings of the pigs.

PRE-SLAUGHTER RESULTS

The piglets were brought into the experimental piggery on 23 December 1936. They were all pure-bred Large Whites from the University Farm herd and during the period of suckling had remained out on

Table IV. *Live-weight gains and meal consumption over experimental period of 14 weeks* (11 *January to* 19 *April*)

		Individually-fed pigs					Group-fed pigs			
Treat-ment	No. and sex of pig	L.w on* 28 Dec. lb	L.w. on 11 Jan. lb.	L.w on 19 April lb.	Total meal consumed lb.	Litter	No. and sex of pig	L.w. on 28 Dec lb.	L.w. on 11 Jan. lb.	L.w. on 19 April lb
Pen I (sow 832)†						Group I (treatment (A)				
A	G 1941	42	53½	183	466·20	832	H 1934	60	72½	211
B	G 1939	45½	56½	185½	478·45	1409	H 1963	44½	56	166½
C	G 1937	48½	64	206	516·95	1409	H 1960	56	68½	183½
C	H 1943	54	69	201	518·35	1412	H 1993	27½	36½	149
B	H 1940	53	68	204½	523·25	117	H 1991	36	47½	148
A	H 1935	48½	61	196	499·10	1126	H 2006	29½	38½	147
						1413	H 1947	62	76	195
Pen II (sow 820)†						820	G 1954	53	66	210
B	G 1957	46	62	197½	503·30	1126	G 2008	28	36½	124
C	G 1956	49½	64	201½	520·45	1413	G 1948	60½	73	181
A	G 1953	48½	62	198	500·85					
C	H 1958	41	52½	170	451·85	Group II (treatment B)				
A	H 1950	65½	82	206	519·85	832	H 1936	59	73½	201½
B	H 1949	45	59	187½	485·80	1409	H 1962	46	59	184
						1409	H 1977	52½	65½	201
Pen III (sow 357)‡						1412	H 1985	44	54	180½
C	G 2002	30½	43	163½	412·65	117	H 1988	33½	41	158
A	G 2001	32½	44	158	397·60	1126	H 2011	24	33½	122½
B	G 1995	31½	37	146	373·45	1413	H 1944	62½	77	218
B	H 1998	31½	43½	143	382·90	820	G 1959	46½	61	193½
C	H 1996	30	41½	141	388·85	1126	G 2007	30	41	138
A	H 1994	34½	44½	146	391·65	1413	G 1946	57½	70½	206½
Pen IV (sow 1408)†						Group III (treatment C)				
C	G 1975	46	60½	188½	503·65	832	H 1938	61	75½	205½
A	G 1972	37½	47	171	433·30	1409	H 1961	48	65	188
B	G 1971	40	52½	187	467·25	1409	H 1965	54	68	197
A	H 1976	42½	53½	176½	490·95	1412	H 1986	37½	52	182
B	H 1970	45½	60½	191	495·95	117	H 1989	40½	55½	177½
C	H 1969	45	62	199½	508·20	1126	H 2005	31	42	151
						1413	H 1933	45½	57½	164½
Pen V (sow 1412)†						820	G 1951	52½	66½	189½
B	G 1983	40	50	174½	448·70	1126	G 2004	28½	38½	157
A	G 1982	38½	49½	179½	446·95	1413	G 1945	58	74	212
C	G 1981	39½	52½	176	458·85					
B	H 1980	38½	51½	168	439·25					
C	H 1979	36½	49	164½	438·55					
A	H 1978	33½	45	148½	391·30					

* Date of distribution; pigs brought on to experimental diets on 30 December.
† Sire: "Histon".
‡ Sire: "Hazels". All the pigs were of the Large White breed. The litters of sows 1408, 1409, 1412 and 1413 were first litters.

Total meal consumed from 11 *January to* 19 *April*

	Individually-fed pigs lb.	Group-fed pigs lb.
By 10 A pigs	4537·75	4537·40
By 10 B pigs	4598·30	4705·05
By 10 C pigs	4718·35	4809·70

Table V. *Average weekly live-weights of pigs during period of comparison*

Treatment	Individually-fed pigs			Group-fed pigs		
	A lb.	B lb.	C lb.	A lb.	B lb.	C lb.
Jan. 11	54·20	54·05	55·80	57·10	57·90	59·45
„ 18	58·95	59·60	62·40	62·60	64·50	66·10
„ 25	65·75	66·55	70·45	68·70	71·10	73·55
Feb. 1	72·85	74·10	78·25	75·25	78·60	81·60
„ 8	80·35	81·80	86·05	82·30	86·40	89·10
„ 15	88·15	90·05	94·55	89·80	94·95	97·65
„ 22	96·95	99·20	103·10	97·80	103·10	105·65
Mar. 1	105·85	108·10	112·15	105·85	111·80	114·20
„ 8	117·35	119·55	122·65	114·90	122·00	124·60
„ 15	124·55	127·55	131·05	123·05	131·65	133·65
„ 22	134·55	136·75	141·05	132·40	141·15	143·15
„ 29	143·60	145·90	150·40	140·20	150·80	152·95
April 5	154·15	155·85	160·45	151·20	159·55	161·85
„ 12	163·90	166·50	170·25	160·30	169·20	171·10
„ 19	176·25	178·45	181·45	171·50	180·35	182·40

Table VI. *Mean rates of live-weight increase and food conversion factors for the period from 11 January to 19 April**

	Individually-fed pigs					Group-fed pigs				
Treat-ment	Range of L.W.I. lb.	Days required	lb. meal consumed by ten pigs	Mean lb. L.W.I. per day	Mean lb meal per lb. L.W.I.	Range of L.W.I. lb.	Days required	lb. meal consumed by ten pigs	Mean lb. L.W.I. per day	Mean lb meal per lb L.W.I.
A	54 20–90	37	1234·30	0·97	3·45	57·10–90	36	1230·85	0·91	3·71
B	54 05–90	35	1167·95	1·03	3·25	57 90–90	31	1064·60	1·04	3·32
C	55·80–90	32	1093·05	1·07	3·20	59 45–90	29	1015·85	1·05	3·33
A	90–150	44	2242·80	1·36	3·74	90–150	46	2324·70	1·30	3·87
B	90–150	45	2299·25	1·33	3·83	90–150	45	2267·20	1·33	3·78
C	90–150	45	2296·70	1·33	3·83	90–150	46	2338·15	1·30	3·90
A	150–176 25	17	1060·65	1·54	4·04	150–171·50	16	981·85	1·34	4·57
B	150–178 45	18	1131·10	1·58	3·98	150–180·35	22	1373·25	1·38	4·52
C	150–181 45	21	1328·60	1·50	4·22	150–182·40	23	1155·70	1·41	4·49
A	54·20–176 25	98	4537·75	1·25	3·72	57·10–171·50	98	4537·40	1·17	3·97
B	54·05–178·45	98	4598·30	1·27	3·70	57·90–180·35	98	4705·05	1·25	3·84
C	55·80–181 45	98	4718·35	1·28	3·76	59 45–182·40	98	4809·70	1·25	3·91

* In this table, for comparative purposes, the data for the individually-fed pigs are accorded the same treatment that for the group-fed pigs, the periods required for the attainment of 90 and 150 lb. live-weight being determined the dates on which the pigs *averaged* these live-weights.

grass with the tethered sows. They were kept after arrival on the standard-protein treatment C during the short period of feeding preceding the grouping of the pigs. The experimental procedure was similar to that adopted in previous trials, and the reader should consult the first paper in this series for the requisite details (Woodman *et al.* 1936).

The distribution of the pigs in the experiment was made on the basis of their live-weights on 28 December. They were brought on to the

experimental rations on 30 December and were weighed again on the mornings of 10, 11 and 12 January 1937, the averages of these three weighings being taken as the initial live-weights in the trial. The comparison of the effects of the three feeding treatments was continued until 19 April (14 weeks), when the first consignment of pigs was sent to the bacon factory, but as in previous trials full records were kept until all the pigs had attained bacon weight at about 200 lb. A summary of the data for live-weight increase and meal consumption over the 14 weeks of comparison is given in Tables IV, V and VI.

Comments on Tables IV, V and VI

The observed differences for the pigs under the different treatments over the 14 weeks of the comparison are:

Treatment	A (low-protein)	B (low-protein)	C (standard-protein)	S.E.
(1) Individually-fed pigs:				
Average lb. L.W.I.	122·05	124·40	125·65	2·04
Average lb. meal consumed	453·8	459·8	471·8	8·00
(2) Group-fed pigs:				
Average lb. L.W.I.	114·40	122·45	122·95	3·73
Average lb. meal consumed	453·7	470·5	481·0	

There were no significant differences between the live-weight gains of the pigs on the different feeding treatments. This finding applies to both the individually-fed and the group-fed pigs and is unaffected when correction is made for differences in the initial live-weights of the pigs. The close agreement between the pigs in treatments B and C should particularly be noted. It is clear that the pigs receiving the standard amounts of white fish meal made no greater live-weight gains over the period of comparison than those receiving rather less than half the standard amounts. It might be inferred from the somewhat lower mean live-weight increase of the group-fed A pigs that the mixture of feeding blood meal, ex. soya bean meal and dried separated milk was not quite so efficient for promoting live-weight increase as the single protein food, white fish meal, but the finding is not significant, and, moreover, the effect is barely to be noted in the case of the individually-fed pigs. This aspect of the results will be referred to again later.

It is of interest to note that the standard error of each pig's live-weight gain in the individual-feeding experiment was 6·43 lb., or 5·18 % of the mean gain. The corresponding results for the group-fed pigs were 11·79 lb. and 9·83 %, from which it may be concluded that the individual-feeding

trial was three-and-a-half times as accurate as the group-feeding test $(9.83^2 \div 5.18^2 = 3.6)$.

The comparative data in Table VI for the mean daily rate of live-weight increase and the efficiency of food conversion, both over the entire period of comparison and during the intermediate stages, emphasize again the agreement between the pigs receiving the standard allowances of white fish meal (treatment C) and those receiving the low supply of this protein food (treatment B). It is also revealed that the A pigs, receiving the low-protein supply in the form of the mixture of protein foods, were slightly less thrifty during the earliest stage of the feeding period up to 90 lb. live-weight, but that they compared very satisfactorily with the B and C pigs during the subsequent stages of the comparison and over the period as a whole. The somewhat poorer progress of the A pigs in the first stage of the feeding trial, particularly during the first two or three weeks (see Table V), may have been due in part to the fact that, after distribution of the piglets among the three feeding treatments on 28 December, the A pigs had to be changed over from a diet containing white fish meal to one containing the mixture of ex. soya bean meal, feeding blood meal and dried separated milk, whereas no such change in feeding was necessary with the B and C pigs, which continued to receive rations containing white fish meal as protein supplement.

The results for the individually-fed pigs are analysed in greater detail in Table VII, the figures this time including the comparisons for the whole period of feeding up to slaughter weight at 200 lb.

Table VII. *Analysis of results for individually-fed pigs (means of results for ten pigs in each treatment)*

	L.w. on 11 Jan. lb.	Up to 90 lb. L.W.			90–150 lb.		
Treatment		Days required	lb. L.W.I. per day	lb. meal per lb. L.W.I.	Days required	lb. L.W.I. per day	lb. meal. per lb. L.W.I.
A	51·11*	39·6	1·00	3·27	44·2	1·36	3·75
B	54·05	34·7	1·05	3·17	45·1	1·34	3·82
C	55·80	31·7	1·11	3·08	45·6	1·32	3·86
S.E.	--	—	0·016	0·05	—	0·018	0·05

		150–200 lb.			Whole trial		
A		34·2	1·47	4·49	115·2	1·27	3·91
B		33·8	1·48	4·43	113·6	1·30	3·86
C		34·4	1·46	4·52	111·7	1·30	3·90
S.E.		—	0·026	0·085	—	0·015	0·05

* Figures for hog 1950 (treatment A) are omitted in the first period, since this animal required only 11 days to reach 90 lb. live-weight; but the figures for this hog are included in all the other periods. Mean live-weight of all ten pigs in treatment A on 11 January was 54·20 lb.

Comments on Table VII

Considering first of all the results of the trial as a whole, it is at once apparent that the figures for mean daily live-weight increase and efficiency of food conversion for the pigs in the three feeding treatments display very close agreement. A similar conclusion may be drawn from the corresponding results in the periods from 90 to 150 lb. and from 150 to 200 lb. live-weight.

The only significant differences are to be found in the earliest stage of the feeding period up to 90 lb. live-weight. During this part of the trial, the mean daily live-weight increase of the B pigs was slightly, though significantly. lower than that of the C pigs, whilst the figure for lb. meal per lb. of live-weight increase was slightly. though in this case not significantly. higher. It may be inferred, therefore, that the inclusion of but 5% of white fish meal in the rations during this early stage did not enable the piglets to display the fullest capacity for growth that was brought out in the pigs receiving 12% of the protein food. This. however, would seem to have been a matter of but little moment, since it is clear from the results in Table VII that the slight initial setback experienced by the pigs on the low level of protein-food intake was fully made up in the subsequent stages of feeding. It may be noted that these findings are in complete harmony with the conclusions drawn from the earlier investigation of this question and recorded in the third paper of this series (Woodman et al. 1939).

It will again be observed that, during the period of feeding up to 90 lb. live-weight. the A pigs receiving the sub-standard allowances of protein food in the form of the mixture of blood meal, dried separated milk and ex. soya bean meal made slightly slower progress than the B pigs receiving the same amounts of protein in the form of white fish meal (see also Table VI for both individually-fed and group-fed pigs). The conditions consequent on the feeding of these low levels of protein food at this early stage should provide a sensitive comparison of the growth-promoting efficiency of the two forms of protein supply. If this be so. it might be concluded that the protein in white fish meal has a slightly higher biological efficiency than the combined proteins in the mixture of protein foods used in treatment A; but part of the difference in the progress of the pigs up to 90 lb. live-weight may have to be ascribed. as has already been explained. to the marked change of ration experienced by the A pigs, but not by the B pigs, when they were brought on to the experimental feeding treatment at the beginning of the trial. In these

circumstances, therefore, it will be safer to state the conclusion as follows: that white fish meal, from the standpoint of protein quality, is at least as good as the mixture of blood meal, dried separated milk and ex. soya bean meal used in this trial.

It is again of interest to note that, despite the slightly lower thriftiness of the A pigs during the period up to 90 lb. live-weight, these animals were able to wipe out almost completely this small initial disadvantage during the later stages of the feeding trial; from which it may be concluded that, considered as pigs to be fed up to bacon weight, they were receiving sufficient protein to enable them to give results, in respect of mean live-weight increase per day and efficiency of food conversion, not significantly different from those shown by pigs receiving the much higher allowances of protein food commonly given in pig-feeding practice.

The results of the group-fed pigs for the whole period up to 200 lb. live-weight bear out the foregoing conclusions from the individual-feeding trial. The C pigs receiving the standard allowances of white fish meal averaged 1·27 lb. of live-weight increase per day as against 1·29 lb. for the B pigs receiving the sub-standard amount of this protein food and 1·23 lb. for the A pigs receiving the sub-standard amounts of the mixture of blood meal, dried separated milk and ex. soya bean meal.

Table VIII. *Effect of feeding treatment on thickness of back fat and belly streak (treatment averages)*

	Back fat*				Belly streak†			
Treatment	(a) mm.	(b) mm.	(c) mm.	Mean mm.	(a) mm.	(b) mm.	(c) mm.	Mean mm.
(1) Individually-fed pigs:								
A	28·2	54·8	39·2	40 7	30·0	38 9	44·3	37·7
B	29·2	56·8	38·5	41·5	28·5	38·4	44·1	37·0
C	26·7	54·5	37·4	39·5	26·5	36·7	45·5	36·2
S.E.	1·27	1·18	1·22	1·04	1·89	0 94	1·05	0·99
Treatment effect	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
(2) Group-fed pigs:								
A	26·7	52·9	34·7	38·1	24·8	35·0	41·5	33·8
B	27·0	54·6	36·1	39·2	27·2	35·0	42·0	34·7
C	25·7	53·2	35·8	38·2	24·1	34·6	43·4	34·0

A, low-protein supply in form of mixture of protein foods; B, low-protein supply in form of white fish meal; C, standard-protein supply in form of white fish meal.

* As measured at (a) the thinnest part along the back, (b) the thickest point at the shoulder and (c) opposite the junction of the third and fourth vertebrae from the curve.

† As measured (a) opposite the curve, (b) opposite the junction of the fourth and fifth vertebrae from the curve and (c) at a distance below (b) equal to the distance from (a) to (b).

Post-slaughter results

The reader is referred to the first paper in this series (Woodman et al. 1936) for a detailed account of the technique of the post-slaughter work. Considerations of space make it undesirable to attempt to record the whole of the measurements on every carcass, and only the treatment averages, together with their standard errors in the case of the individually-fed pigs, are given in the tables.

Comments on Table VIII

The figures for the individually-fed pigs show that the differences of feeding treatment gave rise to no significant differences in the thickness of the back fat and belly streak, a finding that receives confirmation from the results of the group-fed pigs. There is no evidence that the lowering of the supply of protein food to approximately half of that provided in the standard ration had any undesirable effect in respect of back fat and belly streak measurements. From the practical standpoint, it may be noted that the official payment grades, based on similar measurements, showed no bias in favour of the pigs on the standard-protein supply.

Table IX. *Effect of feeding treatment on size and leanness of typical rashers (treatment averages)*

	"Warm" carcass weight lb	Belly rasher*			Mid-back rasher*			Complete rasher*		
		Total† area sq. cm.	Area of		Total† area sq. cm.	Area of		Total† area sq. cm.	Area of	
Treatment			lean sq. cm.	fat sq. cm.		lean sq. cm.	fat sq. cm.		lean sq. cm.	fat sq. cm.
(1) Individually-fed pigs:										
A	160·8	86·58	26·72	57·47	126·02	38·52	81·98	212·60	65·24	112·45
B	161·9	89·00	24·99	60·53	125·77	39·70	83·75	214·77	61·69	141·28
C	159·8	89·53	25·93	61·02	122·33	38·83	80·98	211·86	64·76	112·00
S.E.	--	1·78	0·99	1·69	3·14	1·27	2·63	4·13	2·66	4·01
Effect	-	N.S.	N.S.	N.S.	N.S.	N.S	N.S.	N.S.	N.S.	N.S.
(2) Group-fed pigs:										
A	159·7	84·00	26·12	54·97	118·97	40·12	75·96	202·97	66·24	130·93
B	159·0	81·39	24·51	53·79	114·50	38·77	72·97	195·89	63·28	126·76
C	160·0	82·02	26·60	52·61	112·05	37·91	71·61	194·07	64·54	121·25

A, low-protein supply in form of mixture of protein foods; B, low-protein supply in form of white fish meal, C, standard-protein supply in form of white fish meal.
* See first publication of this series for explanation of these terms (Woodman et al. 1936).
† Total area minus sum of areas of lean and fat equals area occupied by bone

Comments on Table IX

The results for the individually-fed pigs reveal no significant effects of feeding treatment on the size of the typical rashers and the amounts of lean and fat contained in these rashers. The close agreement in these

respects for the group-fed pigs on treatment B (low-protein supply in the form of white fish meal) and treatment C (standard-protein supply in the form of white fish meal) will also be noted. The mean area of the rashers from the group-fed pigs on treatment A (low-protein supply in the form of the mixture of protein foods) was somewhat higher than that of the rashers from the pigs on treatments B and C, but the distinction in this respect was small compared with the range of variation among the animals in any one treatment and did not reach statistical significance.

If the measurements on the typical rashers be taken as a criterion of carcass leanness, it may be concluded that, although the level of protein-food supply was markedly lower in treatments A and B, the pigs on both these treatments gave carcasses that were as lean and well-finished as those produced by the pigs on treatment C containing the standard amounts of white fish meal. This conclusion is further borne out by a consideration of the results in Table X, showing the areas of lean and fat expressed as percentages of the complete rasher, and in Table XI,

Table X. *Fat and lean as percentages of complete rasher*
(treatment averages)

	Individually-fed pigs		Group-fed pigs	
	Lean	Fat	Lean	Fat
Treatment	%	%	%	%
A	30·69	67·00	32·64	64·51
B	30·12	67·18	32·30	64·71
C	30·57	67·02	33·26	64·02

Table XI. *Influence of feeding treatment on "eye" muscle measurements (treatment averages)*

	"Eye" muscle in mid-back rasher					
	Space within line of connective tissue			"Eye" muscle		Back fat opposite "eye" muscle
Treatment	Total area sq. cm.	Area of lean sq. cm.	Area of fat sq. cm.	Length cm.	Depth cm.	cm.
(1) Individually-fed pigs:						
A	33·39	27·23	6·16	7·53	5·59	2·99
B	35·30	29·09	6·21	7·55	5·75	3·08
C	34·01	28·28	5·73	7·82	5·43	2·83
S.E.	0·67	0·66	0·22	—		0·14
Treatment effect	N.S.	N.S.	N.S.	—	—	N.S.
(2) Group-fed pigs:						
A	35·17	29·81	5·36	7·69	5·61	2·63
B	33·70	29·25	4·45	7·54	5·59	2·61
C	33·62	28·31	5·31	7·90	5·36	2·59

in which are recorded the measurements made on the important "eye" muscle.

Comments on Table XI

The results for both the individual-feeding and group-feeding trials point to the conclusion that the differences in protein supply in the three feeding treatments had not affected significantly or even consistently the dimensional characteristics of the "eye" muscle and its content of fat and lean. It is clear that the low-protein treatments A and B contained sufficient protein to enable the "eye" muscle to develop an amount of lean tissue equal to that manifested on the control diet containing the standard allowances of white fish meal. It is further to be observed that the treatment averages for the thickness of the back fat opposite the "eye" muscle also show no significant differences.

Table XII. *Influence of feeding treatment on certain post-slaughter measurements* (treatment averages)

Treatment	(1) Farm-fasted L.W. lb.	(2) L.W. at factory lb.	(3) "Warm" carcass %	(4) Length cm.	(5) Flares g.	(6) Sides as % of carcass weight	(7) Iodine value of back fat
(1) Individually-fed pigs:							
A	201·2	196·9	81·64	75·8	1744	76·22	65·8
B	200·8	196·8	82·27	75·5	1764	75 97	67·4
C	199·6	195·0	81·97	76·4	1802	76·07	69·1
S.E.	· ·	—	0·50	0·54	64·5	0·26	0 51
Treatment effect		—	N.S.	N.S.	N.S.	N.S.	S
(2) Group-fed pigs:							C>B>A
A	202·1	195·9	81·52	76·2	1697	75 44	66·7
B	200·9	195·2	81·45	77 2	1844	75·06	67·1
C	201·4	196·5	81·39	76·9	1773	75·39	68·0

(1) After 24 hr. from previous meal.
(2) After road transport of fasted pigs about 40 miles to bacon factory.
(3) Without applying the allowance for shrinkage on cooling.
(4) As measured from point between first and second ribs to *pubis symphysis*.
(5) Total weight of flares from both sides.
(6) Based on weights of trimmed sides before curing.
(7) Back fat sampled from gammon end of sides (bung fat).

Comments on Table XII

The results for the individually-fed pigs show that the differences of feeding treatment gave rise to no significant differences of conformation in the pigs as judged on the basis of length, carcass percentage and the weights of the sides expressed as percentages of the carcass weights. The group-feeding results are in harmony with this conclusion. It will also be observed that there is no suggestion that the lowering of the protein supply led to an increase in the weight of flare fat.

The treatment averages for the iodine values of the bung fat present an interesting feature. In the case of the individually-fed pigs, the replacement of the mixture of feeding blood meal, dried separated milk and ex. soya bean meal in treatment A by white fish meal in treatment B led to a small, though significant, rise in the iodine value of the bung fat. A further similar rise occurred in the case of the pigs on treatment C, in which the allowance of white fish meal was increased to rather more than double the amount in treatment B. A similar trend is also discernible in the results for the group-fed pigs, although the range of variation is much more restricted in this case.

The effect is probably to be attributed to the difference in the oil content of the protein supplements, which in treatment A was very low. It must be concluded that the highly unsaturated oil in white fish meal, even when this food is used in no more than the standard amounts, may have a slight softening effect on the carcass fat, a finding that emphasizes the importance of the legal specification that white fish meal must not contain more than 6% of oil. The actual oil content of the sample used in the present trials was no more than 3.4%. This result may be contrasted with a recent finding that the fat of meat meal, when this food is used to the extent of no more than 10% of the ration, does not lead to any softening of the carcass fat (Woodman & Evans, 1939).

Whilst it is not suggested that this influence of the oil of white fish meal is of any serious import in pig-feeding practice, provided no more than the customary amounts (see treatment C) are included in the diet, it is of interest to note that the conclusions drawn from the consideration of the iodine values are in general agreement, particularly in respect of the comparison between treatments A and C, with the analysis of the bacon factory verdicts respecting the quality of the fat in the carcasses (Table XIII).

Table XIII. *Analysis of factory opinions on quality of carcass fat*

No. of carcasses with fat adjudicated as:

Treatment	Very firm	Firm	Medium firm
A	5	13	2
B	3	17	—
C	4	11	5

SUMMARY

The present investigation is the sequel to an earlier pig-feeding trial in which a diet supplying only half the standard amounts of protein supplement, in the form of a mixture of feeding blood meal, dried separated milk and ex. soya bean meal, was found to give as good results from the standpoints of rate of growth, efficiency of food conversion and carcass leanness and quality, as a diet that contained the full standard allowances.

It was considered desirable to repeat this initial exploratory experiment, making use this time of a totally different form of protein supplement, since the question of the biological efficiency of the protein supply might conceivably be of critical importance at the lower levels of protein feeding. In the present trial, therefore, the mixture of the three protein foods was replaced by a single protein food, namely, white fish meal. The standard-protein treatment C supplied 12 % of white fish meal up to 90 lb. live-weight, 10 % from 90 to 150 lb., whilst from 150 lb. to slaughter at about 200 lb. live-weight, the white fish meal was omitted from the diet, its place being taken by 5 % of ex. soya bean meal. The corresponding allowances of protein food in the low-protein treatment B were 5, 4 and 3 % respectively. The low-protein treatment A, which was introduced as a link between the previous and the present trials, contained the protein supplement composed of feeding blood meal, dried separated milk and ex. soya bean meal and supplied the same amount of digestible protein as was contained in the low-protein treatment B.

The protein supplements were fed in conjunction with barley, weatings and a small allowance of lucerne meal, and the food supply was scaled so as to reach a maximum of 7 lb. of meal per head per day at about 200 lb. live-weight. The problem was investigated by both the individual-feeding and the group-feeding techniques.

The conclusions from the previous work were completely confirmed by this further investigation. The results of the trial as a whole revealed a close agreement in respect of mean daily live-weight increase and efficiency of food conversion between the pigs on the three feeding treatments. The only significant differences were found in the earliest stage of the feeding period up to 90 lb. live-weight. During this part of the trial, the B and C pigs on the low level of protein-food intake showed a slightly, though significantly, lower mean rate of live-weight increase than the C pigs receiving the standard amounts of protein food, thus confirming the finding in the earlier trial that 5 % of white fish meal (or

its equivalent) is slightly too low at this stage for maximum growth. This, however, would seem to have been a matter of little moment, since the slight initial disadvantage experienced by the low-protein pigs was wiped out during the subsequent stages of the feeding period.

The results also point to the conclusion that the biological efficiency, in relation to growth in the young pig, of the protein in white fish meal is at least as high as that of the combined proteins in the mixture of feeding blood meal, dried separated milk and ex. soya bean meal used as the protein supplement in treatment A.

The pigs on the low levels of protein-food intake gave carcasses showing no significant differences in respect of leanness, conformation and general finish from those obtained from the pigs receiving the standard amounts of white fish meal, a satisfactory finding in view of the fact that this result was achieved without sacrifice in relation to the rate of growth and the efficiency of food conversion.

A subsidiary conclusion from the results of this trial is that the highly unsaturated oil in white fish meal, even when this food is used in no more than the standard amounts, may have a slight softening effect on the carcass fat. The contrast in this respect between white fish meal and meat meal is noteworthy. Although this effect of white fish meal is never likely to be of serious import in pig-feeding practice, provided no more than the customary amounts (see treatment C) are included in pig rations, the result emphasizes the importance of the legal specification that this product must not contain more than 6% of oil, particularly in view of the fact that the sample of white fish meal used in the present trial contained no more than 3·4%.

It is not desirable at this stage to attempt to formulate recommendations for practical pig-feeding on the basis of the results so far obtained. Further trials have already been carried out in which the supply of protein food has been depressed to an even lower level, and balance trials are also being carried out with the object of testing the various findings under more rigid conditions of control than are possible in farm-feeding trials. In a later paper, therefore, the whole of the evidence from this series of trials will be reviewed and its bearing on pig-feeding practice critically examined.

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REFERENCES

WOODMAN, H. E. & EVANS, R. E. (1939). *J. agric. Sci.* **29**, 502.

WOODMAN, H. E., EVANS, R. E., CALLOW, E. H. & WISHART, J. (1936). *J. agric. Sci.* **26**, 546.

WOODMAN, H. E., EVANS, R. E., TURPITT, W. G. & CALLOW, E. H. (1939). *J. agric. Sci.* **29**, 115.

A CRITICAL SURVEY OF BREEDING WHEAT FOR BAKING QUALITY

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(With One Text-figure)

CONSIDERATIONS of quality enter into nearly every breeding programme. More effort has been expended on improving the quality of the wheat grain than that of any other plant product. But in the state of our knowledge of the character which he endeavours to improve, viz. baking quality of wheat, the plant breeder is dependent on the advance of cereal chemistry. This has led him to play a decisive part in various phases of that branch of science, by directing it towards work on methods chiefly suitable for plant-breeding purposes; which of necessity has led to a situation in which empirical methods are attempted as short cuts across a province of research which, fundamentally, was not yet fully explored. On the other hand, genetic studies on wheat quality date back to the first decade of Mendelism. Thus, a review of methodological and genetic problems which have arisen in more than thirty years' breeding for baking quality should permit generalizations extending beyond the realm of wheat breeding.

TESTING WHEAT FOR BAKING QUALITY

The success of any breeding scheme depends largely on the significance and reliability of the methods for determining major and minor differences among breeding units. Three main lines of approach are possible in testing the quality of any plant product, viz. "direct", "indirect", and "analytical".

1. *Direct tests*

Direct tests imitate the process of economic utilization. In the case of wheat, the characteristics of at least a symbol of the finished product—a loaf of bread—are used as the standard of value. The methods range from large-scale commercial baking trials to micro-tests requiring 25 g. of flour (Geddes & Aitken, 1935; Harris & Sanderson, 1938). These tests have in common the baking of a yeast-fermented dough of water, flour and ingredients; but every detail of this involved process is subject to wide variation, adapted to the class of wheat, local conditions and

requirements, etc. A good deal of the criticism which has been levelled against the use of the baking test in plant breeding has been caused by this variety of methods. It must be recognized that the greatly differing characteristics and requirements of wheats render it impossible to recognize the properties of all of them by the application of one single baking procedure; yet, without some common "yardstick", test baking was relegated to the sphere of the "artistic touch" (Blish, 1934).

In recent years determined efforts at standardization have brought a large measure of clarification. The A.A.C.C. test, with its supplementary variations, has created a common basis of reference for the North American Continent. Similar standardized variants of a basic procedure have been introduced by Åkerman (1933) in Sweden, by Hullett in New Zealand, and by Pelshenke (1938b) in Germany. The main feature of this methodological approach is the establishment of a series of baking methods, adapted to the local materials and requirements, which, if used and interpreted conjointly, allow the test baker not only to estimate the baking properties of wheats under the given experimental conditions, but accurately to confer their potentialities (Lamour *et al.* 1933; Geddes & McCalla, 1934; Åkerman, 1933).

Criticisms of the role of the baking test in wheat breeding have been expressed by a number of authors (Shick, 1930; Mader, 1931; Pelshenke, 1933, 1934, 1938; and others). It has been stated that baking tests are expensive and show in execution that they require a large amount of material, that their accuracy and definition is not sufficient, that the personal influence of the baker, both in conducting the test and in its interpretation, invalidates attempts at standardization, and that they supply information only on the complex character—"baking value"—without analytical distinction between its components. To overcome these objections, a number of testing methods have been introduced which are designed to estimate indirectly the baking quality, or, more correctly, some of its components.

II. *Indirect tests*

Commonest among these methods are: (1) the wholemeal fermentation test after Pelshenke and after Cutler & Worzella; (2) the gluten swelling test after Berliner & Koopmann; (3) the Chopin extensimeter; and (4) the Brabender farinograph. The micro-methods described for (1) and (2) can be used on single plants, that for (3) only if the small plants are spaced very widely.

(1), (2) and (3) can be used for the progenies of single plants, and

(4) only at a stage when at least 200 g. of wheat are available. Thus, fermentation, swelling and micro-extensimeter tests can be conducted early in the breeding process; farinograph tests only when material sufficient for baking tests is at the breeder's disposal.

It may be questioned (a) whether the need for quality tests in the earliest stages, viz. in F_2 and in F_3, is as urgent or as general as has frequently been suggested (e.g. Pelshenke, 1933, 1938a; Bayfield, 1935; Engelke, 1935, 1937), (b) whether the accuracy of these tests is sufficient to guarantee that no valuable segregates are lost.

The case for the use of small-scale tests in the early breeding stages is based mainly on the observation that in the majority of crosses high quality apparently is inherited as a multiple recessive, and that consequently homozygous high-quality segregates could be selected directly in F_2. A number of further considerations, however, tend to reduce the significance of this fact:

(1) Quality is hardly ever the only important character: usually improvements in yield, other agronomic characters or disease resistance are also aimed at, and, unless highest quality be indispensable, improvements in any of these features may be highly desirable either to the farmer or to the breeder -as building stones for further work. The chance of finding any such forms would be lost if only the segregates with the highest quality were retained in F_2. In New Zealand, for example, from a cross of the previous standard variety, Tuscan (high yield, low quality) with White Fife (low yield, high quality), a variety was selected with improved resistance to lodging and a yield 11% above that of Tuscan; the quality, however, was not improved. Yet it cannot be questioned that the new variety constitutes an improvement, although admittedly one of the main objectives, high quality, has not been achieved. Such considerations, however, lose their validity when growers of high-quality "premium" wheats are compensated for losses in yield by higher prices. Here selection for quality in F_2, if feasible, seems more promising.

(2) Segregates combining highest quality with agronomic suitability are bound to be very rare in F_2. They are, however, more likely to be found in F_3 families of promising agronomic type segregating for quality.

(3) A reliable small-scale test would be desirable for the selection among the highly homozygous progenies of plants extracted from hybrid mixtures which have been propagated to F_8 or further. It would also be useful in reselecting impure varieties of hybrid origin (Breakwell, 1934) and for the establishment of homozygosity in such varieties.

(4) Any test which is to be applied, as the principal guide for selection, in the early breeding stages, must possess a very high degree of reliability, otherwise the unavoidable natural risks of missing the necessarily very rare combinations of desirable characters would be unduly increased. At this stage the risk of over-valuing—and therefore retaining--unsuitable material is not nearly as grave as that of undervaluing—and therefore discarding—valuable lines. A degree of reliability which may appear sufficient for some purposes of commercial testing (Edel, 1934) need not therefore suffice for the plant breeder.

In the course of ten years' extensive breeding for baking quality at the New Zealand Wheat Research Institute only a small number of lines has been found which combined highest quality with promising agronomic characteristics. Three of these—selected from a back-cross F_1 (Reward × Tuscan) × Tuscan—in general approximate Marquis, the world's standard for quality. Material from variety trials on these lines, extending over a number of years, was tested by various methods and the results afford an opportunity for investigating whether, and if so how frequently, any of these methods might have caused some of the lines to be discarded. The methods used were protein determination, wholemeal fermentation tests after Pelshenke, gluten swelling test, farinograph and baking tests (two formulae, viz. without and with potassium bromate) (Table I). Included in this series also were Marquis, Tuscan, a variety of medium-low quality, and Lin Calel, an Argentine wheat which, under New Zealand conditions, gives a quality varying from the highest to the lowest grades. The results were arranged in classes (Table II) which attempted to render the observed differences in a comparative order. The highest mark, 1, was given to the best variety in the individual test and trial, the other varieties being classed according to their relative performances. The classes can be interpreted as follows:

1	Good	⎫
2	Good	⎬ Likely to be retained in selection.
3	Fairly good ⎱ Medium	
4	Rather poor ⎰	
5	Poor	⎫
6	Poor	⎬ Liable to be discarded in selection.
7	Very poor	⎭

Omitting protein content, only 64,03 returned in all tests scores of 3 or higher. The results for Tuscan, Marquis, 64,02 and 64,04 are illustrated in Fig. 1. Results below the thick horizontal lines are liable to lead to

Table I. Results of tests for baking quality

Protein content

Variety	1937-8			1938-9						
	Lincoln	Amberley	Methven	Waikari	Yaldhurst	Lincoln	Winchmore	Lyndhurst	Lyalldale	Gleniti
Tuscan	9·2	8·5	9·4	9·0	8·9	9·7	9·5	8·2	9·75	8·6
Lin Calel	—	—	—	8·1	8·2	9·0	9·4	7·8	9·6	8·8
Marquis	9·8	8·4	10·5	8·8	9·0	9·7	10·2	8·1	10·5	9·5
64,02	9·3	8·8	10·7	9·6	8·5	9·8	10·0	8·9	9·9	9·3
64,03	9·7	9·4	10·1	9·1	9·1	9·7	8·8	8·4	9·8	9·3
64,04	9·8	8·8	10·9	9·1	9·4	9·7	9·8	9·1	9·7	9·6

Wholemeal fermentation time test (after Pelshenke)

Variety	1935-6	1937-8		1938-9						
	Lincoln	Amberley	Methven	Waikari	Yaldhurst	Lincoln	Winchmore	Lyndhurst	Lyalldale	Gleniti
Tuscan	58	42	44	28	25	18	36	24	37	32
Lin Calel	—	—	—	30	32	30	60	27	47	54
Marquis	72	64	121	58	39	44	78	24	55	51
64,02	87	58	78	66	56	66	76	67	79	52
64,03	77	71	141	55	62	62	65	61	75	58
64,04	71	69	83	34	38	37	78	50	73	57

Gluten swelling test 1938-9

Variety	Waikari	Yaldhurst	Lincoln	Winchmore	Lyndhurst	Lyalldale	Gleniti
Tuscan	11·0	6·0	7·0	4·5	11·0	14·0	6·0
Lin Calel	14·0	6·0	8·0	6·0	9·0	13·0	12·0
Marquis	14·0	12·0	14·0	15·0	8·0	12·5	14·0
64,02	23·0	19·0	18·8	18·8	18·8	20·0	21·0
64,03	16·0	14·0	15·0	11·0	13·0	23·0	15·0
64,04	12·0	16·0	13·0	13·0	12·0	14·0	12·0

Baking tests

Variety	Baking method	1936-7 Lincoln	1937-8 Lincoln	1937-8 Amberley	1937-8 Methven	1938-9 Waikari	1938-9 Yaldhurst
Tuscan	Control	19, g.	32, m., g.s. +	25, g.	25, g.,g.s.	11, sl.o.m., p.s.	9, v.g., dead
	Bromate	26, sl.g.	30, o.m., g.s. -	22, b.o.m., p.s.	24, o.m., a.s.	11, b.o.m., p.s.	9, v.g., dead
Lin Calel	Control	—	—	—	—	13, sl.o.m., p.s.	11, o.m., v.p.s.
	Bromate	—	—	—	—	13, b.o.m., p.s.	11, o.m., v.p.s.
Marquis	Control	32, o.m.	34, v.g., e.s.	30, g., g.s. -	33, g., e.s.	26, g., g.s.	23, sl.g., v.f.s.
	Bromate	33, o.m.	39, m., e.s.	30, o.m., g.s. -	38, m., e.s.	28, sl.o.m., g.s.	23, sl.o.m., v.f.s.
64, 02	Control		36, g., v.g.s.	33, sl.o.m., g.s. +	37, m., e.s.	16, m., f.s.	18, m., p.s.
	Bromate	36, g.	38, m., e.s.	29, o.m., g.s.	30, o.m., v.g.s.	21, sl.o.m., f.s.	18, sl.o.m., p.s.
64, 03	Control	20	34, sl.g., g.s. +	26, sl.g., g.s.	36, m., e.s.	22, m., g.s.	18, sl.g., f.s.
	Bromate	29, sl.g.	36, m., v.g.s. +	27, o.m., g.s. -	38, sl.o.m., e.s.	23, sl.o.m., v.f.s.	17, sl.o.m., f.s.
64, 04	Control	36, g.	35, m., e.s.	28, o.m., e.s. -	36, m., e.s.	17, b.o.m., v.f.s.	21, g., f.s.
	Bromate	37, sl.o.m.	36, m., e.s.	26, b.o.m., g.s. -	39, sl.o.m., e.s.	16, v.b.o.m., v.f.s.	18, o.m., f.s.

1938-9

Variety	Baking method	Lincoln	Winchmore	Lyndhurst	Lyalldale	Gleniti
Tuscan	Control	9, sl.g., p.s.	16, v.g., f.s.	10, o.m., v.p.s.	19, v.g., g.s.	21, v.g., f.s.
	Bromate	12, m., p.s.	22, sl.g., v.f.s.	12, b.o.m., v.p.s.	28, m., g.s.	21, g., f.s.
Lin Calel	Control	12, o.m., p.s.	24, m., v.f.s.	12, sl.o.m., p.s.	26, m., v.g.s. +	25, m., g.s. +
	Bromate	12, b.o.m., p.s.	23, b.o.m., v.f.s.	14, o.m., p.s.	—	—
Marquis	Control	28, sl.g., g.s.	27, g., v.s.	12, m., f.s.	27, g., v.g.s. +	25, v.g., g.s.
	Bromate	23, o.m., v.g.s.	34, o.m., v.g.s.	12, o.m., f.s.	30, m., v.g.s. +	30, sl.g., g.s.
64, 02	Control	33, m., v.g.s.	27, g., g.s.	19, m., f.s.	27, sl.g., v.g.s.	29, m., g.s.
	Bromate	35, m., v.g.s.	33, m., g.s.	29, m., f.s.	—	—
64, 03	Control	29, sl.g., v.g.s.	27, g., g.s.	26, sl.g., g.s.	29, g., v.g.s.	27, v.g., g.s.
	Bromate	33, m., g.s.	35, m., g.s.	27, m., f.s.	30, m., v.g.s.	33, m., g.s.
64, 04	Control	26, o.m., v.f.s.	26, g., g.s.	27, g., v.f.s.	25, sl.g., v.g.s.	33, m., g.s.
	Bromate	24, o.m., v.f.s.	32, m., g.s.	28, o.m., g.s.	—	—

Explanation of baking tests in Table I

The figure is the "baking score" (highest score: 50). Next follows the report on the correctness of the fermentation of the dough; finally observations of dough strength made during handling of the fermented dough.

Abbreviations

Fermentation
g.bd. = gluten bound   (highly under-fermented)
v.g. = very green
g. = green
sl.g. = slightly green
m. = mature
sl.o.m. = slightly overmature
o.m. = overmature
b.o.m. = badly overmature
v.b.o.m. = very badly overmature (highly over-fermented)

Strength
e.s. = excellent
v.g.s. = very good
g.s. = good
a.s. = average
v.f.s. = very fair
f.s. = fair
p.s. = poor
v.p.s. = very poor
dead

Table II. *Results of tests for baking quality, grouped in classes*

Protein content

Variety	1937-8			1938-9						
	Lincoln	Amberley	Methven	Waikari	Yaldhurst	Lincoln	Winchmore	Lyndhurst	Lyalldale	Gleniti
Tuscan	3	4	6	3	2	1	3	4	3	4
Lin Calel	.	.	.	6	6	3	3	5	4	3
Marquis	1	4	2	3	2	1	1	4	1	1
64,02	2	3	1	1	4	1	1	1	3	2
64,03	1	1	3	2	2	1	5	3	3	2
64,04	1	3	1	2	1	1	2	1	3	1

Wholemeal fermentation time test

Variety	1935-6	1937-8			1938-9						
	Lincoln	Lincoln	Amberley	Methven	Waikari	Yaldhurst	Lincoln	Winchmore	Lyndhurst	Lyalldale	Gleniti
Tuscan	4	5	4	5	5	5	6	5	5	5	3
Lin Calel	.	.	.	.	5	4	5	3	5	4	1
Marquis	2	3	2	1	2	2	3	1	5	3	1
64,02	1	3	3	2	1	2	1	1	1	1	1
64,03	2	2	1	1	2	1	1	2	1	1	1
64,04	2	2	2	2	4	4	4	1	3	1	1

Gluten swelling test 1938-9

Variety	Waikari	Yaldhurst	Lincoln	Winchmore	Lyndhurst	Lyalldale	Gleniti
Tuscan	4	4	4	5	3	2	4
Lin Calel	3	4	4	4	3	2	3
Marquis	3	3	2	2	4	3	2
64,02	1	1	1	1	1	1	1
64,03	3	2	2	3	2	1	2
64,04	4	2	2	2	3	2	3

Baking test

Variety	1936-7 Lincoln	1937-8 Lincoln	1937-8 Amberley	1937-8 Methven	1938-9 Waikari	1938-9 Yaldhurst	1938-9 Lincoln	1938-9 Winchmore	1938-9 Lyndhurst	1938-9 Lyalldale	1938-9 Gleniti
Tuscan	4	4	4	5	6	7	7	6	6	3	4
Lin Calel	·	·	·	·	5	6	7	4	5	1	2
Marquis	1	1	1	1	3	1	3	1	3	1	1
64,02	1	1	1	1	3	4	1	2	1	1	1
64,03	1	2	1	1	2	2	2	1	1	1	1
64,04	2	1	1	1	3	2	4	2	1	1	1

Farinograph test

Variety	1935-6 Lincoln	1936-7 Lincoln	1937-8 Lincoln	1937-8 Amberley	1937-8 Methven	1938-9 Waikari	1938-9 Yaldhurst	1938-9 Lincoln	1938-9 Winchmore	1938-9 Lyndhurst	1938-9 Lyalldale	1938-9 Gleniti
Tuscan	4	4	5	5	5	5	5	5	4	4	3	5
Lin Calel	1	1	·	·	·	3	3	3	3	2	2	1
Marquis	1·5	1	2	1	1	2	1	2	1	1	2	1
64,02	1·5	1·5	2	1	1	1	1	1	2	1	2	1
64,03	2	2	3	2	2	1	1	1	1	1	2	1
64,04	2	2	3	2	2	3	3	3	2	1	2	2

Strength figure in baking test

Variety	1937-8 Lincoln	1937-8 Amberley	1937-8 Methven	1938-9 Waikari	1938-9 Yaldhurst	1938-9 Lincoln	1938-9 Winchmore	1938-9 Lyndhurst	1938-9 Lyalldale	1938-9 Gleniti
Tuscan	3	4	4	4	6	5	3	5	3	3
Lin Calel	1	·	·	4	5	5	2	4	1	1
Marquis	1	2	1	2	3	2	1	2	2	1
64,02	2	1	1	2	2	1	1	2	2	1
64,03	1	2	1	2	2	2	1	2	2	1
64,04	1	2	1	2	2	3	1	2	2	1

Fig. 1. Results of quality tests on four varieties of wheat, grouped in quality classes.

the loss of the variety. The average protein contents of Tuscan and Lin Calel are lower than those of the other wheats, and in these it rarely drops below the horizontal line. Yet the number of tests in which the protein content of Tuscan rises above this line leads to the conclusion that protein determination, under New Zealand conditions, cannot be used as a principal basis of selection.

The remaining methods, however, clearly establish the superiority of the four high-quality wheats over Tuscan and Lin Calel; yet, whilst the general impression rendered by the multiplicity of trials is clear, there are a number of tests in which the quality wheats score below the horizontal line. The frequencies of such observations are recorded in Table III.

Table III. *Frequency of results liable to lead to losses of valuable material*

	Marquis		64,02		64,04	
	Abs.	%	Abs.	%	Abs.	%
Fermentation test	1	9	1	9	3	27
Gluten swelling test	1	14	0	0	1	14
Baking test	0	0	1	9	1	9
Strength score	0	0	0	0	0	0
Farinograph	0	0	0	0	0	0

Of the methods applied the most reliable were the farinograph and the observation of "strength" in the baking process; whilst fermentation and gluten swelling tests led to an appreciable proportion of errors. Two out of the five fermentation tests scoring under 3 exhibit also a low swelling test record. Seasonal variation of results obtained by means of the fermentation time test has been noted by a number of authors (Frankel & Donald, 1933; Vettel & Pelshenke, 1934; Boerger, 1937). Cutler & Worzella (1933) and Griffiths & Cayzer (1934) suggest that such tests should be repeated for several years, thereby admitting their doubtful value for F_2 and F_3 selection.

(5) In many breeding programmes a higher degree of definition is required than one capable of differentiating extremes of quality. Minor improvements may be highly acceptable, and few breeders are prepared to disregard every line falling short of the ideal. Yeoman II is noted as a marked improvement on the quality of the average English wheat, in New Zealand as well as in England. Yet results of wholemeal fermentation tests on Yeoman, in comparison with typical English wheats, were as follows:

	1932–3	1935–6
Yeoman II	31	27
Squarehead's Master	24	20
Webb's New Harvester	28	24

Differences of this order having no true significance, Yeoman might have been discarded had selection followed on the lines of such results. Moreover, in farinograph tests Yeoman as a rule resembles weak varieties.

The further a breeding scheme has advanced towards achieving high quality, the greater the degree of differentiation it requires in its testing methods. The above-mentioned cross, Tuscan × White Fife, yielded a variety, "Cross 7", whose quality is intermediate between that of the parents. If for purposes of further improvement Cross 7 and White Fife were crossed, no indirect method would afford sufficiently reliable differentiation among the resulting lines (cf. also Aamodt & Torrie, 1935).

Specificity of gluten quality among high-quality wheats cannot be ascertained by simple, indirect tests. Hullett considers that Jumbuck, an Australian wheat grown in New Zealand, is specifically different in baking behaviour from other strong wheats, and that it is particularly valuable in certain blends. This difference has been ascertained only in baking tests; it failed to appear in any of the indirect tests.

How far are indirect tests able to meet the objections raised against the baking test?

(1) *Amount of material, speed and expense.* The labour and time efficiency of the tests which have been carried out extensively at the Wheat Research Institute are as follows:

Wholemeal fermentation time test: two men carry out 150 tests (in duplicate) per day; 15 g. of wheat required.

Gluten swelling test: two men carry out 50 tests per day; 10 g. of flour required.

Farinograph test: one man carries out 25 tests per day; 100 g. of flour required for Junior bowl.

Baking test: two experienced test bakers carry out 90 tests per day (usually sufficient to test at least 45 wheats); 125 g. of flour required per test.

The first and second methods are quicker and cheaper and demand appreciably less space and labour in the field. It may be questioned, however, whether the economic factor of the testing problem should receive much consideration. It is suggested, in view of the great values at stake, that the organization of breeding and testing should be adapted to suit the most reliable and significant methods, rather than that one should accept methods suited to an existing type of organization.

(2) *The personal factor.* It should be recognized that the success of the baking test depends largely on the skill and experience of the test baker, both in conducting and in interpreting the test. Yet the baking

test is capable of a large degree of standardization. In New Zealand a system of staff exchanges and of checking by means of standard samples has achieved a high degree of uniformity between testing laboratories. On the other hand, the personal factor is not absent from those indirect tests which are not responsive to full mechanization. Thus, the results of the gluten swelling test and those of the fermentation test (Bayfield, 1935) are liable to modification by the individual influence of the operator. In the farinograph test the operation is strictly standardized, but the interpretation of the results is to a certain extent subjective.

(3) *Analytical value.* Indirect tests aim at measuring mainly that component of baking value which is chiefly amenable to improvement by plant breeding, viz. "baking strength". This character, which is believed to depend largely on the quantity and the quality of the gluten, is open to approach by means of chemical and physical methods. The "indirect" methods, however, are based on assumptions of analogies between processes arrived at empirically and certain phenomena believed to occur in the baking procedure. They are backed by correlations with other indirect tests, with baking tests, or with practical experience. In no case are the phenomena underlying indirect tests fully understood and theories which endeavour to explain them have hardly been put to the test. The wholemeal fermentation time test, for example, consists of the immersion into water of a dough ball whose disintegration is timed. These experimental conditions are far enough removed from those of the baking process to require an explanatory theory which can be proved or disproved by other than statistical methods. Until recently the only theories recorded suggested a leaching of salts into the water causing collapse (Saunders & Humphries, 1928) or an action of proteolytic enzymes and the hydrolytic action of the distilled water on the gluten (Bayfield, 1935). Swanson (1937), Swanson & Dines (1929) and Swanson (1939) investigated the influence of a number of variations and additions. Results to date indicate that in addition to gluten quality, proteases and protease inhibitors and activators influence the "time". These factors may remove time differences between "strong" and "weak" wheats.

Our present state of knowledge on the foundation of indirect tests leads to the conclusion that the analytical nature of the information which can be gleaned by an experienced test baker from a close observation of the dough and of the finished loaf is hardly inferior to that obtainable from "indirect" tests.

III. *Analytical tests*

These attempt to assess baking behaviour in terms of physical constants and chemical constituents. Schofield, Scott-Blair and Halton have shown that relative strengths of flours can be satisfactorily expressed by a relationship between the viscosity and the elasticity modulus of doughs prepared under certain conditions. The investigations of these workers have been directed towards discovering the fundamental physical properties required in a good flour dough. Whilst the chief merit of this work is to provide an approach to the physical fundamental of dough behaviour, it is probable that in their practical application these investigations will lead to instruments suitable for routine testing. The Research Association of British Flourmillers and Brabender G.M.B.H. have both independently devised instruments to which these principles can be applied, and the Wheat Research Institute in New Zealand is working on an instrument suitable for micro-tests.

Ultimately, all dough phenomena must be referred to their chemical bases. The physical methods afford the accuracy of description required for the chemical approach, such as the work of Jorgensen and others on proteolytic activity, and of McKellar and co-workers on the fractionation of gluten.

THE INHERITANCE OF BAKING QUALITY

The significance of studies on the inheritance of quality is limited by that of the methods of its determination. A number of authors, starting with Biffen (1908), used kernel structure or nitrogen content. More recently, fermentation time, micro-swelling and micro-extensimeter tests have been applied. Many authors state that high quality is recessive and based on a number of polymerous factors (Pelshenke, 1932, 1933; Rosenstiehl, 1934; Engelke, 1937; Méneret, 1937). The author, using the fermentation time test, found a prevalence of high-quality F_3 families in crosses of Jumbuck (high quality) × Tuscan (low quality), and Reward × Tuscan. Worzella (1934) suggested three dominant factors for quality in the cross Trumbull × Michikoff. A genetic analysis of quantitative characters is practicable, and valuable for the breeder, when accurate measurement is possible. So far such analyses have been confined to characters admitting direct estimation by number, weight or measurement; but it is to be expected in a character of the extreme complexity of baking quality that inheritance studies will yield indeterminate and contradictory results. They are applicable only to the

material studied and do not permit of general conclusions. A genetic approach to quality is dependent upon an analysis of its fundamentals.

Conclusions and summary

1. For both genetical and methodological reasons, tests for quality, in the majority of breeding schemes, are not required at the early stages of the breeding process.

2. Reliability and definition of any one empirical test is not sufficient to safeguard against losses of valuable material.

3. It is suggested, therefore, that as a rule agronomically promising lines should be carried on to a stage where comprehensive tests, using a number of selected methods, can be carried out, preferably over a number of seasons. It may be questioned whether a combination of such tests as the wholemeal fermentation and the gluten swelling tests (Pelshenke, 1938a) would suffice. In the light of the available evidence a testing system might be suggested comprising baking tests together with such "indirect" and, better still, "analytical" methods as will afford accurate information of an analytical nature.

4. This review of the testing problem suggests the conclusion that empirical tests are limited in their significance and reliability, and that only an increased knowledge of the fundamentals can afford a truly scientific approach. It should be admitted that the plant breeder, with his insistence on empirical tests where fundamental knowledge was lacking, has side-tracked the cereal chemist from the narrow path of scientific approach all too often. It is questionable whether this has been to the ultimate advantage of wheat breeding.

5. Inheritance studies on quality should greatly facilitate the task of the breeder. They will become feasible and valuable only when the nature of the desirable characters and the true significance of the testing methods are clearly understood.

REFERENCES

AAMODT, O. S. & TORRIE, J. H. (1935). *Canad. J. Res.* **13**, 79–88.

ÅKERMAN, A. (1933). *Mühlenlab.* Spec. Suppl. 1933.

BAYFIELD, E. G. (1935). *J. Amer. Soc. Agron.* **27**, 241–50.

BIFFEN, R. H. (1908). *J. agric. Sci.* **3**, 86–101.

BLISH, M. J. (1934). *Cereal Chem.* **11**, 70-3.

BOERGER, A. (1937). *Arch. Fitotécn. Uruguay,* **2**, 1–84.

BREAKWELL, E. J. (1934). *J. Dep. Agric. S. Aust.* **37**, 1532–9.

CUTLER, G. H. & WORZELLA, W. W. (1933). *Cereal Chem.* **10**, 250–62.

EDEL, P. (1934). *Mühle,* **71** (Suppl.).

ENGELKE, H. (1935). *J. Landw.* **83**, 89–106.

—— (1937). *Landw. Jb.* **84**, 779–98.

FRANKEL, O. H. & DONALD, H. P. (1933). *Proc. World's Grain Exhib. and Conf. Canada,* **2**, 133.

GEDDES, W. F. & AITKEN, T. R. (1935). *Cereal Chem.* **12**, 696–707.

GEDDES, W. F. & McCALLA, A. G. (1934). *Cereal Chem.* **11**, 384–95.

GRIFFITHS, E. L. & CAYZER, L. S. (1934). *Agric. Gaz. N.S.W.* **45**, 14–17.

HARRIS, P. H. & SANDERSON, T. (1938). *Cereal Chem.* **15**, 251–6.

LARMOUR, R. K., GEDDES, W. F. & WHITESIDE, A. G. O. (1933). *Cereal Chem.* **10**, 601–4.

MADER, W. (1931). *Zuchter,* **3**, 286–97.

MÉNERET, G. (1937). *C.R. Acad. Agric. Fr.* **23**, 742–7.

PELSHENKE, P. (1932). *Z. Zücht. A,* **18**, 1–18.

—— (1933). *Cereal Chem.* **10**, 90–6.

—— (1934). *Zuchter,* **6**, 169-72.

—— (1938*a*). *Zuchter,* **10**, 6–9.

—— (1938*b*). *Mühlenlab.* **8**, 194–8.

ROSENSTIEHL, K. V. (1934). *Züchter,* **6**, 261–2.

SAUNDERS, H. A. & HUMPHRIES, S. (1928). *J. nat. Inst. agric. Bot.* **2**, 34.

SCHICK, R. (1930). *Züchter,* **2**, 72–80.

SWANSON, C. O. (1937). *Cereal Chem.* **14**, 419-33.

—— (1939). *Cereal Chem.* **16**, 365–76.

SWANSON, C. O. & DINES, F. T. (1939). *Cereal Chem.* **16**, 168-77.

VETTEL, F. & PELSHENKE, P. (1934). *Zuchter,* **6**, 193–9.

WORZELLA, W. W. (1934). *J. agric. Res.* **49**, 705–14.

OBSERVATIONS ON THE MINERAL METABOLISM OF PULLETS. IV

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THE experiments described in the present paper were concerned with the nature of the calcium and phosphorus combinations present in the droppings of pullets and involved investigation of the extent to which inositolhexaphosphoric acid (phytic acid) present in the food of pullets receiving various diets may be recovered from the droppings.

Some years ago Halnan (1925) suggested that tricalcic phosphate is the chief phosphorus compound normally present in the droppings of non-laying pullets, but his experimental results are susceptible of other interpretations (Common, 1933).

Knowles *et al.* (1933) reinvestigated the problem by analysing the droppings of non-laying pullets which were receiving rations deemed to be adequate in calcium and phosphorus. When the calcium equivalent to the carbonate content of the fresh droppings was subtracted from the total calcium content of the droppings, it was found that the residual calcium was nearly equal to the total phosphorus content of the droppings multiplied by 1·29; in other words each atom of residual calcium corresponded to one atom of total phosphorus. For convenience this relation will be referred to in the present paper as "Knowles's rule". It should be remarked that the relation was put forward only for non-laying pullets receiving adequate amounts of calcium carbonate: the droppings of such birds normally contain carbonate.

Knowles *et al.* concluded from their results that the non-laying pullet receiving a ration adequate in calcium carbonate excretes its phosphorus as dicalcic phosphate, any calcium in excess of that necessary to form this salt being excreted as calcium carbonate. Only traces of water-soluble phosphate were detected in the droppings of their birds.

Neither Halnan nor Knowles *et al.* directed any special attention to the possibility that some of the phosphorus in the droppings might have been in organic combination. Very little work has been carried out on the possible significance of organic phosphorus in poultry nutrition,

although Lowe *et al.* (1939) have recently shown that the phosphorus of phytic acid is less efficient than the phosphorus of sodium phosphate in correcting a rachitogenic ration of high Ca/P ratio.

If phytic acid is not completely broken down in the alimentary tract of the fowl, then phytic acid compounds were probably present in the droppings of the birds investigated by Knowles *et al.* The presence of even a considerable amount of the phosphorus of the droppings in this form would not of itself invalidate "Knowles's rule"; the ratio Ca/P for calcium inositolhexaphosphate precipitated in the intestine might well be the same as the ratio Ca/P for dicalcic phosphate. However, "Knowles's rule" was shown to hold for only three different rations in which the ratio Ca/P ranged within rather narrow limits (1·49–1·90) and none of the birds in the experiments were laying. It seemed desirable, therefore, to test the validity of the rule for wider dietary Ca/P ratios, and for laying as well as for non-laying birds.

PRELIMINARY EXPERIMENTS

Several preliminary balance experiments were carried out in order to see whether or no the pullet has special powers of hydrolysing phytic acid. Three non-laying pullets were placed in metabolism cages and given an exclusive diet of wheat grain. After a preliminary period of 7 days the amounts of phytic acid in the droppings were compared with the amounts ingested in the grain. The experimental results are set out in Table I. The analytical methods are described in a subsequent part of the paper.

Table I. *Recovery in dried droppings of phytic acid
of wheat fed to pullets*

Pullet	No. of days	Wheat eaten g.	Phytic acid P in wheat mg.	Phytic acid P in droppings mg.	$\dfrac{\text{Phytic acid P in droppings}}{\text{Phytic acid P in food}} \times 100$
1	7	453·7	1171	381	32·5
2	7	585·1	1510	520	34·4
3	7	700·0	1806	637	35·3

These results demonstrated that the droppings of the non-laying pullet may contain a considerable proportion of the phytic acid consumed in its food. In a similar experiment where the pullet was allowed to eat oyster-shell grit, 53·6 % of the phytic acid of the wheat was recovered from the droppings. Similar observations were made on birds receiving a diet of maize meal.

EXPERIMENT I

In the light of the preliminary experiments further metabolism experiments were carried out during 1938.

The immediate objects were (a) to reinvestigate the validity of "Knowles's rule" using various rations, and (b) to investigate the recovery in the droppings of phytic acid present in the food when a certain ration was supplemented with calcium carbonate or tricalcic phosphate.

Scheme of experiment

Six White Wyandotte pullets of the same strain were selected. The birds were all about 6 months of age. Day-to-day balances were conducted with these birds using two groups of rations. The first group included three rations mixed so as to imitate the three rations used by Knowles *et al.* (1933). The basal meal mixture for these rations consisted of four parts yellow maize, three parts fine pollard, two parts Sussex ground oats and one part finely ground extracted soya bean meal. The rations themselves were then made up as follows:

Ration A	Ration B
800 g. basal meal mixture	800 g. basal meal mixture
44 g. precipitated calcium phosphate	26·5 g. precipitated calcium phosphate
7·5 g. precipitated chalk	21 g. precipitated chalk
4 g. salt	16 g. "Phytin"
	4 g. salt

Ration C	Ration D
1000 g. basal meal mixture	1000 g. basal meal mixture
62·9 g. precipitated chalk	50 g. tricalcic phosphate
62·9 g. "Phytin"	5 g. salt
5 g. salt	

The "Phytin" was calcium magnesium inositolhexaphosphate as manufactured by Messrs Ciba, Basle, and sold by them under the trade name "Phytin".

The other group of experimental rations was made up as follows:

	Ration CR	Ration PR
Maize meal	25	25
Ground wheat	25	25
Fine pollard	25	25
Sussex ground oats	12½	12½
Extracted soya bean meal	12½	12½
Cod-liver oil	2	2
Salt	½	½
Calcium carbonate	5	--
Tricalcic phosphate	--	5

Note. "CR" signifies carbonate ration, and "PR" signifies phosphate ration.

The cod-liver oil was a reputable brand guaranteed to contain not less than 1000 international units vitamin A and 100 international units vitamin D per g. The tricalcic phosphate was "calcium triphosphoricum exsiccatum, Merck".

The average analyses of these six rations are given in Table II.

Table II. *Average analyses of rations used in Exp. I*

	Ca		P		Phytic acid P		Mg.
	%	c.v.	%	c.v.	%	c.v.	%
Ration A	2·160	1·77	1·542	2·11	0·488	3·08	0·221
Ration B	2·213	2·50	1·529	1·48	0·800	5·06	0·253
Ration C	2·833	2·18	1·698	2·13	1·472	1·58	0·286
Ration D	1·694	1·74	1·425	1·64	0·484	4·24	—
Ration CR	1·961	1 36	0·543	2·56	0·410	3·00	0·218
Ration PR	1·765	1·29	1·415	1·41	0·424	3·26	0·210

The coefficient of variation (c.v.) covers both sampling and analytical errors since the samples were drawn at random throughout the course of the experiment. The coefficient of variation is greatest for the phytic acid determinations; this is most probably due to greater experimental error in this determination.

Experimental technique

The birds were housed in specially designed metabolism cages, particular attention being paid to the design of the feeding troughs.

The birds were fed at 9.30 a.m. and 4.00 p.m. each day. The daily ration was regulated to just below appetite, and the daily intake of food was kept as constant as possible. Distilled water only was offered to the birds for drinking.

Rations CR and PR were prepared in pellet form since comparatively large amounts of these rations were required. The other rations were carefully mixed by hand in small lots and stored in waxed cartons.

The droppings were collected each morning at 9 a.m. in tared Pyrex pie dishes, mixed thoroughly to a soft pasty consistency with addition of water if necessary and weighed. 10 g. of the wet mass were weighed out at once into Collins's calcimeter flasks for the carbonate determination. The dishes were then placed in an electric oven and quickly brought to 100° C. to inactivate all enzymes. Drying was completed overnight in an air oven at 60–70° C. The total weight of dried droppings was readily calculated from the final dry weight and the original wet weight, since exactly 10 g. of the fresh droppings were removed before drying.

Eggs were prepared for analysis by a very convenient method kindly

communicated to the writer by Mr E. T. Halnan of the School of Agriculture, Cambridge. The egg was broken into a large evaporating dish and whipped to a frothy mass. The shell was then crushed as finely as possible and whipped into the mass, which was dried overnight in the electric oven at 100° C. and finally ground to a powder in an Empressa no. 69 hand mill. Aliquots of the powder were weighed out for analysis.

Analytical methods

Calcium was determined volumetrically (Godden, 1937). Total phosphorus was determined by an application of the method of Fiske & Subbarrow (1925) which has been described elsewhere (Common, 1936).

Phytic acid P was determined by the method of McCance & Widdowson (1935), but with two main modifications. Dry ashing in the presence of excess calcium acetate was adopted instead of wet combustion, and the method of Fiske & Subbarrow (1925) was used for the determination of phosphorus. The modified method gave very satisfactory results when tested for recovery of sodium phytate P from pure solution or from cereal extracts.

Magnesium was determined gravimetrically; the precipitate of magnesium ammonium phosphate was reprecipitated under standard conditions and weighed as such after air-drying to constant weight (Jones, 1916).

Carbonate was determined by the Collins's calcimeter; due regard being paid to the correction necessary for the volume of the sample of fresh droppings. In those instances where the carbonate thus determined was very low, it was possible that a proportion of the gas liberated consisted of gases other than carbon dioxide. Experiment showed that the carbonate determination must be carried out on the fresh droppings; drying always resulted in loss of carbon dioxide, due in part at least to volatilization of ammonium carbonate from calcium carbonate and ammonium urate.

Live weights of birds during Experiment I

The birds remained in excellent health and condition throughout the experiment and their live weights are recorded in Table III. Pullet 2 did not lay, and her live weight remained fairly steady with a tendency to rise later. All the other birds laid to a greater or less extent and this is reflected in the varying live weights. Birds under such experimental conditions do not gain much in weight when laying, and the record of live weights is very satisfactory.

Table III. *Live weights of experimental birds in kg.*
Exp. I began on 29 *December* 1937

| | No. of experimental bird | | | | | |
| | 1 | 2 | 3 | 4 | 5 | 6 |
Date						
29. xii. 37	2·55	2·45	2·20	2·64	2·42	2·65
7. i. 38	2·38	2·45	2·24	2·62	2·30	2·68
14. i. 38	2·28	2·46	2·36	2·77	2·25	2·59
21. i. 38	2·56	2·57	2·50	2·81	2·57	2·88
28. i. 38	2·63	2·48	2·61	2·79	2·64	2·87
4. ii. 38	2·41	2·47	2·50	2·61	2·40	2·75
11. ii. 38	2·36	2·46	2·45	2·55	2·39	2·65
18. ii. 38	2·35	2·45	2·50	2·60	2·35	2·67
25. ii. 38	2·35	2·47	2·56	2·61	2·45	2·68
4. iii. 38	2·48	2·62	2·64	2·68	2·36	2·74
11. iii. 38	2·46	2·76	—	2·65	2·32	—

Experimental results

The full experimental data of the day-to-day balances are too extensive for complete presentation so that only cumulative data for periods are reported.

It is convenient to discuss first the composition of the droppings; the relevant data are set out in Table IV. In this table are given the total phosphorus and calcium in the droppings, the carbonate calculated as calcium carbonate, the "non-carbonate calcium" (calculated by difference) and the value of the figure for total phosphorus × 1·29. In addition the data for total phytic acid phosphorus found in the dried droppings, and for total calcium and phosphorus metabolism are reported.

Table IV shows that a considerable proportion of the phosphorus in the droppings of pullets may be in the form of phytic acid. In the case of ration C about three-quarters of the total phosphorus in the dried droppings was in the form of phytic acid. These facts do not of themselves invalidate "Knowles's rule", which merely states that, in the droppings of non-laying pullets receiving adequate calcium carbonate, the total calcium less the carbonate calculated as calcium equals the total phosphorus × 1·29. Knowles *et al.* interpreted this rule as meaning that the non-laying pullet receiving adequate calcium carbonate excreted phosphorus in the form of dicalcic phosphate, the excess calcium being excreted as carbonate. The present experiments show that this is only one possible interpretation of the rule.

The next consideration is the question of the validity of "Knowles's rule". It will be seen from Table IV that the results with pullets 2 and 3 on rations A and B are in close accord with the rule; in fact, the day-to-

Table IV. *Exp. 1. Summary of experimental results*

Composition of droppings

No. of bird	Ration	Experimental period days	No. of eggs produced	P g.	Ca g.	Carbonate calculated as CaCO₃ g.	Non-carbonate calcium g.	P × 1.29 g.	Phytic acid P g.	Ca,P ration	Ca,P droppings	Phytic acid P in food g.	Phytic acid P recovery in droppings %
3	A	16	1	21·58	28·06*	0·82	27·24	27·83	5·41	1·40	1·30	7·76	69·7
2	B	13	0	12·87	18·03†	2·00	16·03	16·60	5·82	1·45	1·40	7·60	76·6
3	C	13	6	20·84	23·34‡	4·33	19·01	26·88	15·61	1·67	1·29	19·10	81·7
4	CR	7	0	3·09	9·24	5·25	3·99	3·99	2·23	3·61	2·99	2·99	74·6
4	CR	13	10	7·31	12·00	6·18	5·83	9·43	4·57	3·61	1·64	5·62	81·3
1	CR	21	13	12·23	16·91	7·32	9·54	15·77	6·84	3·61	1·38	9·23	74·1
5	CR	21	14	13·28	19·50	10·78	8·72	17·22	7·03	3·61	1·47	9·23	76·2
6	CR	21	15	11·77	15·45	7·32	8·14	15·17	6·77	3·61	1·31	9·23	73·4
1	PR	21	10	25·28	15·14	0·53	14·61	32·61	4·79	1·25	0·60	9·11	52·6
4	PR	21	6	30·27	24·56	0·82	23·74	39·05	5·12	1·25	0·81	9·79	52·3
5	PR	21	15	28·34	16·66	0·56	16·10	36·56	5·38	1·25	0·59	9·53	56·5
6	PR	7	5	9·44	5·71	0·15	5·56	12·18	1·76	1·25	0·60	3·26	54·0
2	D	16	0	15·27	16·52	0·32	16·20	19·69	3·21	1·19	1·08	5·86	54·8

Balance data

No. of bird	Ration	Experimental period days	No. of eggs produced	Ca In food g.	Ca Retained g.	Ca In eggs g.	Ca Nett balance g.	P In food g.	P Retained g.	P In eggs g.	P Nett balance g.
3	A	16	1	34·35	6·29	1·87	4·42	24·52	2·94	0·12	2·82
2	B	13	0	21·02	2·99	0·0	2·99	14·52	1·65	0·0	1·65
3	C	13	6	36·76	13·43	13·20	0·23	21·99	1·13	0·72	0·41
4	CR	7	0	14·29	5·05	0·0	5·05	3·96	0·87	0·0	0·87
4	CR	13	10	26·87	14·87	18·81	−3·94	7·44	0·13	1·20	−1·07
1	CR	21	13	44·12	27·21	27·25	−0·04	12·21	−0·01	1·36	−1·35
5	CR	21	14	44·12	24·62	29·98	−5·36	12·21	−1·06	1·54	−2·60
6	CR	21	15	44·12	28·67	29·19	−0·52	12·21	0·45	1·79	1·34
1	PR	21	10	37·97	22·83	19·42	3·41	30·44	5·16	1·05	4·11
4	PR	21	6	40·78	16·22	11·48	4·74	32·70	2·43	0·67	1·76
5	PR	21	15	39·69	23·03	26·67	−3·64	31·82	3·48	1·70	1·78
6	PR	7	5	13·59	7·89	8·12	−0·23	10·90	1·46	0·57	0·89
2	D	16	0	20·52	4·00	0·0	4·00	17·26	1·99	0·0	1·99

Note. Carbonate determinations on fresh droppings; all other determinations on dried droppings.
* Contained also 3·32 g. Mg.   † Contained also 2·12 g. Mg.   ‡ Contained also 3·52 g. Mg.

day agreement was also very good and these results are in full agreement with the observations of Knowles *et al.* Very considerable traces of water-soluble phosphate were found in the droppings of pullet 3 on ration A, but only traces in the case of pullet 2 on ration B.

The results with pullet 3 on ration C do not accord with "Knowles's rule"; the non-carbonate calcium was always much less than the total phosphorus × 1·29, although the droppings always contained appreciable amounts of carbonate. The droppings contained practically no water-soluble phosphate in spite of the fact that this bird was laying.

In the case of pullets 1, 5 and 6 on ration CR the non-carbonate calcium of the droppings is again much smaller than the total phosphorus × 1·29, although the ratios Ca/P for the droppings are similar to the corresponding ratios in the experiments of Knowles *et al.* The same considerations apply to the results secured with pullet 4 on ration CR during her non-laying period. With regard to water-soluble phosphate, fair traces were present in the droppings of pullets 1, 5 and 6 on numerous occasions in approximate association with the periods of active shell formation.

It seemed probable from the results that "Knowles's rule" might hold for non-laying pullets but not for laying pullets. This surmise was supported by the fact that while the droppings of pullet 4 did not obey the rule during an initial laying period, they showed close accordance with the rule during a subsequent short non-laying period of 7 days.

The results with pullets 1, 4, 5 and 6 on ration PR are completely at variance with the rule, but in these cases the phosphorus content of the food was very high, calcium was being deflected to shell formation and the Ca/P ratio of the droppings was much lower than 1·29. It was not surprising to find that the droppings under these circumstances contained abundant water-soluble phosphate. This group of results does not invalidate "Knowles's rule", for the birds were laying and the amounts of carbonate in their droppings were very small and of doubtful significance.

Whether the percentage recovery in the droppings of ingested phytic acid is to be related to apparent digestibility of phytic acid is dependent on the validity of the assumption that no hydrolysis of phytic acid took place during the drying of the droppings. It will be shown below that such hydrolysis was probably negligible.

The percentage recovery of phytic acid is highest of all in the case of ration C, being 81·7 % of the intake. This is not surprising, for this ration contained a high percentage of phytic acid both absolutely and

relatively to the total phosphorus percentage, while the calcium percentage in the ration was also high. The recovery was 76·6 % in the case of ration B and 69·7 % in the case of ration A.

Comparing the results with pullets 1, 4 (laying period), 5 and 6 on ration CR with those for the same pullets on ration PR it will be noted that the percentage recovery is considerably greater in the case of ration CR, i.e. 73–81 % as against 52–56 %. If it be taken that no hydrolysis of phytic acid took place during the drying of the droppings, then this difference might be due to either (a) the greater calcium content of ration CR or (b) the greater effect of calcium carbonate as compared with calcium phosphate in lowering the apparent digestibility of phytic acid.

In the case of pullet 4 the percentage recovery of food phytic acid in the droppings was 74·6 % during the non-laying period as against 81·3 % during the laying period.

Tentative conclusions from Exp. I

The following tentative conclusions were drawn from the experiment of 1938:

(1) Phytic acid in the food is not completely hydrolysed in the alimentary tract of the pullet, and may account for a significant proportion of the total phosphorus in the droppings.

(2) "Knowles's rule" is valid for non-laying birds on rations of a certain Ca/P ratio, but is not necessarily valid for laying birds receiving the same rations.

(3) The percentage recovery in the dried droppings of phytic acid present in the food was greater when a particular ration was supplemented with calcium carbonate than when the supplement was tricalcic phosphate. This suggested that calcium carbonate might inhibit alimentary hydrolysis of phytic acid to a greater extent than tricalcic phosphate.

EXPERIMENT II

The results from the experiments just described were somewhat fragmentary, and it was therefore decided to make further experiments with the following objects:

(a) To see if "Knowles's rule" held for ration C when the pullet was not laying, and if it did not hold for rations A and B when the pullet was laying.

(b) To verify whether "Knowles's rule" held for ration CR when the

pullets were not laying, since the previous evidence on this point was very slight.

(c) To investigate the recovery of ingested phytic acid of the basal part of rations A, B and C when the sole mineral supplement was (1) salt and (2) salt plus 5 parts calcium carbonate per 100 parts basal ration.

(d) To investigate more closely the effect of calcium on percentage recovery of phytic acid when the calcium was given as (1) carbonate and as (2) phosphate by making the percentage calcium the same in both rations and using non-laying birds.

Rations A^1, B^1, C^1, CR^1 and PR^1 were made up in the same way as rations A, B, C, CR and PR in Exp. I, except that the amount of tricalcic phosphate included in ration PR^1 was adjusted so that the calcium content of ration PR^1 was the same as the calcium content of CR^1. Ration BR consisted of 100 parts of the basal meal mixture plus 0·5 part salt, and ration BRC consisted of 100 parts basal meal mixture plus 0·5 part salt plus 5 parts precipitated chalk.

The analytical data for these rations are set out in Table V.

Table V. *Analyses of rations used in Exp. II*

Ration	%	c.v.	%	c.v.	Phytic acid P %	c.v.	Mg. %
A^1	2·144	0·99	1·572	2·60	0·451	5·28	0·228
B^1	2·222	1·83	1·519	2·12	0·782	4·51	0·256
C^1	2·844	1·31	1·688	1·54	1·409	3·38	0·301
BR	0·079	3·83	0·625	1·19	0·474	2·97	0·244
BRC	1·876	1·46	0·602	1·27	0·458	3·84	0·229
CR^1	1·877	1·35	0·537	1·77	0·392	3·11	0·224
PR^1	1 869	1·19	1·415	2·64	0·404	2·73	0·214

Note. Ration BR had the following composition per cent: moisture 11·73, ether extract 4·80, crude protein 15·92, nitrogen-free extract 58·92, crude fibre 5·17, ash 3·46.

It will be seen from Table V that the rations in this experiment were very similar in analysis to those used in Exp. I.

The experimental birds were spring-natched White Wyandotte pullets purchased from a dealer. The birds were not in lay when brought under experimental conditions, but were believed to have laid previously. They were in moderate condition when purchased, but improved steadily in general condition throughout their period of confinement.

All experimental details were as already described for Exp. I.

Live weights of birds during Exp. II

The live weights of the birds during Exp. II are set out in Table VI. Pullets 8, 9 and 10 did not lay during the experiment, and their live

weights accordingly show a small steady increase. Pullet 7 laid a few eggs but this did not prevent her from making a small steady increase. Pullet 11 laid in the latter weeks of experiment when on ration BRC, and this is reflected in a slight terminal decrease. Pullet 12 laid throughout and her live weight decreased slightly.

Table VI. *Live weights of experimental birds in kg.*
Exp. II began on 10 *January* 1939

	No. of experimental bird					
Date	7	8	9	10	11	12
8. i. 39	2·38	2·06	1·89	2·24	1·83	—
15. i. 39	2·43	2·10	1·97	2·27	1·88	1 81
22. i. 39	2·43	2·19	2·04	2·33	1·90	1 87
28. i. 39	2·43	2·24	2·11	2·40	1·95	1·79
5. ii. 39	2·48	2·37	2·16	2·47	2·00	1·77
12. ii. 39	2·51	2·40	2·22	2·54	2·04	1 77
19 ii. 39	—	·	··	—	1·95	1·74
26. ii. 39	—	—	··	—	1·93	··

Experimental results

The experimental results are set out briefly in Table VII. The first point to which attention may be directed is the fact that "Knowles's rule" does not hold for rations A^1 and B^1 for laying birds, a result which was not unexpected and which follows in any case from the low Ca/P ratio of the droppings. The non-carbonate calcium is much smaller than the total phosphorus × 1·29 in both cases. Water-soluble phosphate was frequently present in the droppings chiefly in association with shell formation.

The results with ration C for a non-laying pullet did not, however, accord well with "Knowles's rule". At first sight this appeared unsatisfactory, but on consulting the data of Knowles *et al.* it will be seen that they secured poorer agreement between non-carbonate calcium and total phosphorus × 1·29 in the case of ration C than in the cases of rations A and B. Knowles *et al.* sought to explain this greater discrepancy in the case of ration C on the grounds of its greater magnesium content owing to the magnesium present in the comparatively large supplement of phytin used in this ration. This magnesium, they suggest, might play a similar role to calcium in the droppings; if present as carbonate, then it would have the effect of making the determined non-carbonate calcium slightly low; if as phosphate, then the figure for total phosphorus × 1·29 would be too large.

However, ration BR, which consisted of the basal mixture plus 0·5 %

salt, contained 0·244 % magnesium, and ration C^1 contained 0·301 % magnesium. It is not easy to see how this magnesium may be invoked in order to bring the results more closely into accord with "Knowles's rule".

If it is assumed that magnesium is all excreted in much the same ways as calcium, then it will be permissible to calculate the magnesium in the droppings from the pullets on ration C^1 as calcium and add this in with the total calcium. When this calculation is made in the case of the experiment with ration C^1 then the figure for non-carbonate calcium is increased to 24·39 g. which is in good agreement with the figure for total phosphorus × 1·29, i.e. 23·40. If the same calculation is made for the droppings secured from the birds on rations A^1 and B^1, it is true that better agreement with "Knowles's rule" is secured but a large discrepancy still exists. Moreover, a similar calculation applied to the droppings in the case of rations A and B in the experiment of 1938 would have had the effect of destroying the accord with "Knowles's rule" instead of improving it; this may be seen from the magnesium contents of the droppings in question, which are given in Table IV. It would be possible to calculate in several instances the amount of magnesium necessary to bring the results into accord with "Knowles's rule", and thus fractionate the magnesium of the droppings, but such a course assumes the validity of the rule and leaves the mode of excretion of the remaining magnesium quite vague.

With regard to water-soluble phosphate, none was found in the droppings from pullet 11 when fed on ration C^1.

Turning to the results secured with ration CR^1 and non-laying pullets (nos. 8, 9 and 10), it will be seen that in each case the non-carbonate calcium is *greater* than the figure for phosphorus × 1·29. If any attempt is made to correct for the magnesium in the droppings, this disagreement will be intensified. Water-soluble phosphate was almost completely absent from the droppings of these birds when receiving ration CR^1.

In the case of pullet 7, which laid three eggs, there is a fair agreement, the non-carbonate calcium being somewhat smaller than the total phosphorus × 1·29, but the correction for magnesium destroys the agreement completely.

In the case of pullet 12, which laid five eggs, agreement when on ration CR^1 is poorer than in the case of pullet 7, the non-carbonate calcium being much smaller than the total phosphorus × 1·29; at the same time the correction for magnesium secures fair agreement in the case of pullet 12.

Table VII. Exp. 11. Summary of experimental results

Composition of droppings

No. of bird	Ration	Experimental period days	No. of eggs produced	P g.	Carbonate calc. as CaCO₃ g.	Non-carbonate calcium g.	P × 1·29 g.	Mg g.	Non-carbonate calcium Mg calc. as Ca g.	Phytic acid P g.	Ca/P ration	Ca:P droppings g.	Phytic acid P in food g.	Phytic acid P recovery in droppings %
12	A¹	7	4	9·49	0·32	7·83	12·24	1·31	10·10	2·30	1·36	0·88	3·16	72·8
12	B¹	14	8	16·47	0·90	11·25	21·25	2·61	15·76	7·19	1·46	0·74	10·56	68·1
11	C¹	15	0	18·14	12·34	19·24	23·40	3·00	24·39	14·44	1·68	1·74	17·79	81·7
8	CR¹	15	0	7·27	13·47	11·24	9·38	2·95	16·31	4·60	3·49	3·40	5·50	83·6
9	CR¹	15	0	7·36	13·49	11·57	9·49	2·90	16·56	4·36	3·49	3·40	5·64	77·3
10	CR¹	15	0	6·48	12·40	10·15	8·36	2·91	15·15	4·67	3·49	3·48	5·68	82·2
7	CR¹	15	3	6·51	9·53	7·89	8·40	2·23	11·73	3·38	3·49	2·68	4·29	78·8
12	CR¹	14	4	3·74	4·51	2·80	4·82	1·48	5·34	2·01	3·49	1·95	3·34	60·2
7	PR¹	15	0	18·88	25·10	24·27	24·36	2·81	29·11	3·88	1·32	1·33	5·67	68·4
8	PR¹	7	0	8·68	0·70	10·78	11·19	1·41	13·20	1·74	1·32	1·33	2·83	61·5
9	PR¹	15	0	19·40	0·43	25·60	25·03	2·87	30·53	3·39	1·32	1·34	5·62	60·3
10	PR¹	15	0	19·77	0·60	26·66	25·50	2·72	31·33	3·81	1·32	1·38	5·70	66·8
11	BR	15	0	7·90	0·45	1·26	10·19	2·98	6·39	1·72	0·13	0·22	7·11	24·2
11	BRC	12	6	5·93	3·96	6·37	7·65	2·14	10·05	3·45	4·10	1·74	5·50	62·7

Balance data

No. of bird	Ration	Experimental period days	No. of eggs produced	Ca In food g.	Ca In eggs g.	Ca Re-tained g.	Ca Nett balance g.	P In food g.	P Re-tained g.	P In eggs g.	P Nett balance g.	Mg In food g.	Mg Re-tained g.	Mg In eggs g.	Mg Nett balance g.
12	A¹	7	4	15·01	6·16	6·66	0·50	11·00	1·51	0·47	1·04	1·60	0·29	0·12	0·17
12	B¹	14	8	30·02	14·72	17·87	3·15	20·52	4·05	0·92	3·13	3·46	0·85	0·18	0·67
11	C¹	15	0	35·92	0·00	4·34	4·34	21·34	3·20	0·00	3·20	3·80	0·80	0·00	0·80
8	CR¹	15	0	26·34	0·00	1·63	1·63	7·54	0·27	0·00	0·27	3·14	0·19	0·00	0·19
9	CR¹	15	0	26·99	0·00	1·93	1·93	7·72	0·36	0·00	0·36	3·22	0·32	0·00	0·32
10	CR¹	15	0	27·18	0·00	4·63	4·63	7·78	1·30	0·00	1·30	3·24	0·33	0·00	0·33
7	CR¹	15	3	20·55	5·59	3·13	-2·46	5·88	-0·63	0·30	-0·93	2·45	0·22	0·08	0·16
12	CR¹	14	4	15·99	7·91	8·68	0·77	4·57	0·83	0·54	-0·29	1·91	0·43	0·09	0·34
7	PR¹	15	0	26·25	0·00	1·15	1·15	19·88	1·00	0·00	1·00	2·81	0·20	0·00	0·20
8	PR¹	7	0	13·08	0·00	1·50	1·50	9·91	1·23	0·00	1·23	1·50	0·09	0·00	0·09
9	PR¹	15	0	25·98	0·00	-0·05	-0·05	19·67	0·27	0·00	0·27	2·98	0·11	0·00	0·11
10	PR¹	15	0	26·35	0·00	-0·91	-0·91	19·95	0·16	0·00	0·16	3·02	0·30	0·00	0·30
11	BR	15	0	1·19	0·00	-0·52	-0·52	9·38	1·48	0·00	1·48	3·66	0·67	0·00	0·67
11	BRC	12	6	22·55	11·56	12·22	0·66	7·22	1·29	0·67	0·62	2·75	0·61	0·18	0·43

Note. Carbonate determined on fresh droppings; all other determinations made on dried droppings.

Water-soluble phosphate was found in the droppings of pullets 7 and 12 in association with the periods of shell formation, but was almost absent during the non-laying periods.

In the case of the droppings from pullets 7, 8, 9 and 10 when on ration PR[1], there is good agreement with "Knowles's rule", but the amounts of carbonate in the droppings were very small and it seems likely that the agreement follows from the Ca/P ratios of droppings and food being not greatly different from 1·29. Water-soluble phosphate was present in the droppings in considerable quantities.

In the case of the period on ration BR there is no agreement with "Knowles's rule", but no agreement would be expected on a ration of such low calcium content. It was hardly surprising to find plenty of water-soluble phosphate in the droppings. Agreement is better in the case of ration BRC, although the non-carbonate calcium is somewhat smaller than the figures for phosphorus × 1·29; if the magnesium in the droppings is reckoned as calcium, then the "non-carbonate Ca" becomes considerably larger than the phosphorus × 1·29. Here again water-soluble phosphate was found in the droppings.

It seems evident from the considerations put forward above that the magnesium content of the droppings cannot be used in any consistent way in order to explain the deviations from "Knowles's rule" encountered in the present experiments.

If the evidence of Exps. I and II be now considered together, then it may fairly be said that the results confirm the observations of Knowles *et al.* in so far as they deal with non-laying birds receiving rations similar to the rations used by these workers. Where the work is extended to include a ration (i.e. ration CR[1]) of higher Ca/P ratio than A, B, C, or A[1], B[1] and C[1], then agreement with "Knowles's rule" is no longer found, neither does the rule appear to hold strictly for laying birds.

It seems very probable that "Knowles's rule" holds for non-laying pullets for a certain range of dietary Ca/P ratio when the calcium supplement is in the form of carbonate. How the rule is to be interpreted is a different matter; it might be interpreted to mean that calcium and phosphorus are being excreted as calcium phytate, dicalcic phosphate and calcium carbonate. This interpretation, however, does not account for the excretion of magnesium and the picture is further complicated by the possible occurrence of calcium sulphate in the fowl's droppings. In the cases of pullets 8, 9 and 10 when on ration CR[1], it seems quite feasible that some of the calcium, magnesium and phosphorus were being excreted as inositolhexaphosphates and most of the remainder as a

mixture of inorganic phosphates of greater average basicity than dicalcic phosphate, i.e. some such mixture as occurs in freshly prepared "precipitated calcium phosphate". In the case of laying birds the whole position is complicated by day-to-day fluctuations in the composition of the mineral constituents of the droppings due to the Ca/P metabolism of egg production. There is some evidence that ammonium phosphate may at times account for part of the water-soluble phosphate in the droppings of the laying pullet (Common, 1936).

The recovery of ingested phytic acid in the droppings in Exp. II was of the same order as in Exp. I. The recovery was 72·8 % in the case of ration A[1] as against 69·7 % for ration A, and 68·1 % for ration B[1] as against 76·6 % for ration B. For ration C[1] recovery was 81·7 %, the same as for ration C in Exp. I (81·7 %).

In the case of the experiments using rations CR[1] and PR[1] it is evident that the percentage recovery of phytic acid was considerably higher in the case of these rations than in the case of rations CR and PR; this might mean that the apparent digestibility of phytic acid may be higher in the case of laying birds than in the case of non-laying birds on certain rations, possibly because of the decrease in the amount of calcium in the alimentary tract at the times of rapid shell formation with a consequent smaller tendency to formation of insoluble phytates. The actual percentage recoveries in the case of ration CR[1] are of the same order as the percentage recovery in the case of ration C.

From a comparison of the recoveries in the cases of rations CR[1] and PR[1], it is evident that the percentage recovery was much smaller when calcium was added to the ration as tricalcic phosphate than when it was added as calcium carbonate. This is clearly a phosphate effect, for in the case of rations CR[1] and PR[1] the calcium contents were the same. The effect appeared whether the birds were laying or no.

The possibility that this decrease in percentage recovery of phytic acid was due to a varying degree of hydrolysis of phytic acid during drying of the droppings from rations CR[1] and PR[1] was not overlooked. The following experiment suggests that any such hydrolysis is not appreciably affected by presence of excess calcium carbonate in the droppings.

The droppings from a bird receiving ration PR[1] were carefully mixed to a fine paste. Of this 100 g. were taken and mixed with 5 g. precipitated calcium carbonate. The droppings thus treated as well as the untreated droppings were then dried by the method described above. If droppings treated in the usual way have the same ratio of phytic acid phosphorus

to total phosphorus, then it might appear reasonable to assume that the amount of hydrolysis during drying, if any, is to a large extent at least independent of the amount of calcium carbonate in the droppings. The results of this experiment are set out in Table VIII and suggest that the differences in percentage recovery of phytic acid on ration CR[1] as compared with ration PR[1] are not due to inhibition of hydrolysis of phytic acid by calcium carbonate during drying of the droppings.

Table VIII. *Phytic acid phosphorus in droppings dried with and without addition of carbonate*

	Total P %	Phytic acid P %	Ratio Phytic acid P / Total P
Droppings P	1·992	0·294	0·15
Droppings P + $CaCO_3$	1·520	0·226	0·15
Droppings Q	1·672	0·172	0·10
Droppings Q + $CaCO_3$	1·356	0·147	0·11
Droppings R	1·616	0 362	0·22
Droppings R + $CaCO_3$	1·240	0·311	0·25
Droppings S	1·408	0·267	0·19
Droppings S + $CaCO_3$	1·128	0·218	0·19

Whether or not hydrolysis occurs during drying of excreta does not appear to have been investigated by either McCance & Widdowson (1935) or Young (1936) or Lowe & Steenbock (1936). Accordingly experiments were conducted on this point. A bird was fed on ration BR. The droppings were collected and very thoroughly mixed to a stiffish paste with distilled water. 5 g. portions were weighed out at once for the direct determination of total phosphorus and phytic acid phosphorus. The remainder of the droppings were dried in the manner described above. As may be seen from Table IX the ratio of phytic acid P/total P did not appear to be altered appreciably by drying, even in the case of a ration so poor in calcium as ration BR.

Table IX. *Effect of drying on ratio of phytic acid P/total P in droppings*

	1st day	2nd day	3rd day	4th day
Phytic acid P in fresh droppings mg. per g.	1·42	1·66	1·41	1·22
Total P in fresh droppings mg. per g.	4·06	4·53	3·86	4·35
Phytic acid P in fresh droppings / Total P in fresh droppings	0·35	0·37	0·37	0·28
Phytic acid P in dried droppings mg. per g.	6·10	6·64	6·66	5·27
Total P in dried droppings mg. per g.	17·52	19·04	18·88	19·52
Phytic acid P in dried droppings / Total P in dried droppings	0·35	0·35	0·35	0·27

These results make it very probable that the percentage recovery of

phytic acid in dried droppings in the present experiments was a satisfactory measure of the apparent digestibility of phytic acid.

A comparison of the results secured with ration BR and ration BRC indicates that calcium carbonate has a powerful effect in limiting hydrolysis of phytic acid in the alimentary tract of the fowl, for the recovery is much higher with ration BRC even although the bird was laying during the period on this ration. Lowe & Steenbock (1936) have demonstrated a similar effect of calcium carbonate on phytic acid metabolism in the case of the rat.

The present experiments give no information as to the way in which hydrolysis of phytic acid is effected in the alimentary tract of the fowl. The available evidence suggests that endogenous digestive enzymes are not responsible, for Lowe & Steenbock (1936) could not detect a phytase in the intestinal mucosa of the chicken.

At the same time cereals contain phytase. Adler (1915) found that the optimum pH for plant phytase is about pH 5·4. Since the crop contents of the fowl may develop an acidity as high as pH 4·0 (Kerr & Common, 1935), it is not unlikely that some hydrolysis may be effected in the crop by this exogenous phytase. Lowe & Steenbock (1936) have furthermore drawn attention to the possibility that the intestinal flora may be responsible for phytase activity in the intestinal tract.

The presence of excess calcium might affect the degree of hydrolysis either by rendering phytic acid insoluble through formation of calcium phytates or by altering the intestinal flora. Phytic acid, in so far as it remains unhydrolysed, may decrease the availability of calcium by formation of calcium phytate; experiments in support of this view have been reported by Young et al. (1935) and by Harrison & Mellanby (1939). The problem of the role of phytic acid in calcium-phosphorus metabolism involves consideration of several factors, including enzyme activity, bacterial activity and solubility as affected by the relative amounts of various anions and cations present in the alimentary tract as well as by hydrion concentration.

In conclusion it may be pointed out that Titus et al. (1937) have proposed a formula based on "Knowles's rule" as a means of estimating the calcium requirements of laying hens. The present experiments suggest that the theoretical basis of this method of calcium limitation may require reconsideration, although Titus et al. report a satisfactory agreement with the results of practical laying trials.

Summary

1. Phytic acid in cereals and in certain rations based on cereals was incompletely hydrolysed during its passage through the intestinal tract of the pullet.

2. The percentage recovery in the droppings of phytic acid in a ration (24·2 %) based on cereals plus extracted soya bean meal was considerable even when the ration included no calcium supplements. Both calcium carbonate and tricalcic phosphate greatly increased the percentage recovery. A supplement of calcium carbonate led to a somewhat higher recovery of phytic acid than a supplement of tricalcic phosphate containing the same amount of calcium.

3. The recovery of phytic acid tended to be somewhat higher in laying birds than in non-laying birds; this may have been associated with decreased amounts of calcium in the alimentary tract due to the demands for egg-shell formation.

4. The observations of Knowles *et al.* on the composition of the droppings of non-laying pullets on certain rations were confirmed; it was found, however, that their rule connecting the amounts of carbonate, calcium and phosphorus in such droppings did not extend (*a*) to the case of laying pullets, or (*b*) to certain other rations of wider Ca/P ratio.

5. The interpretation of the rule enunciated by Knowles *et al.* to mean that calcium and phosphorus are normally excreted by the pullet as dicalcium phosphate and calcium carbonate was shown to be untenable in view of the fact that the droppings may obey this rule and yet contain considerable amounts of phosphorus in organic combination.

REFERENCES

ADLER, L. (1915). *Biochem. Z.* **70**, 1.

COMMON, R. H. (1933). *J. agric. Sci.* **23**, 555.

—— (1936). *J. agric. Sci.* **26**, 85.

FISKE, C. H. & SUBBARROW, Y. (1925). *J. biol. Chem.* **46**, 375.

GODDEN, W. (1937). *Tech. Commun. Bur. Anim. Nutrit., Aberd.*, **9**, 10.

HALNAN, E. T. (1925). *J. nat. Poult. Inst.* **10**, 410.

HARRISON, D. C. & MELLANBY, E. (1939). *Biochem. J.* **33**, 1660.

JONES, W. (1916). *J. biol. Chem.* **25**, 87.

KERR, W. & COMMON, R. H. (1935). *Vet. Rec.* **91**, 309.

KNOWLES, F., WATKIN, J. E. & HENDRY, F. W. F. (1933). *J. agric. Sci.* **23**, 196.

LOWE, J. T. & STEENBOCK, H. (1936). *Biochem. J.* **30**, 1991.

LOWE, J. T., STEENBOCK, H. & KRIEGER, C. H. (1939). *Poult. Sci.* **18**, 40.

McCANCE, R. A. & WIDDOWSON, E. M. (1935). *Biochem. J.* **29**, 2694.

TITUS, H. W., BYERLY, T. C., ELLIS, N. K. & NESTLER, R. B. (1937). *Poult. Sci.* **16**, 118.

YOUNG, L. (1936). *Biochem. J.* **30**, 252.

YOUNG, L., GREGORY, R. A. & VERE-JONES, N. W. (1935). *J. Soc. chem. Ind., Lond.*, **54**, 270.

DISTRIBUTION OF MANGANESE IN THE PEA SEED IN RELATION TO MARSH SPOT

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(With One Text-figure)

THE disease, marsh spot, which is confined to the seed of the culinary pea, *Pisum sativum*, has been known for a very long time, and its occurrence is noted yearly in certain districts in this country and elsewhere in Europe, especially Holland. Attempts by several workers to find the cause of the disease have failed to associate either fungi or bacteria, and inoculation experiments by Miss Lacey (1934) have indicated that the disease is not of virus origin. More recent efforts have, therefore, been concentrated on examining the possibility of a physiological cause. Trials were carried out in Holland by de Bruijn (1933) to test the influence of the more commonly used manures, but the results were either negative or inconclusive. Ovinge (1935) in Holland and Furneaux & Glasscock (1936) in this country made extensive surveys of marsh spot soils and were able to correlate the occurrence of the disease with certain soil types in the areas surveyed. It was suggested by Löhnis (1936) and Pethybridge (1936) that the cause of the disease was an insufficiency of available manganese in the soil, and work has progressed in both countries to test this hypothesis. Ovinge (1938) claimed to have obtained complete control of the disease in field-plots by late applications of manganese, while Lewis (1939) found that spraying the foliage with a solution of a manganese salt at flowering time gave much better control of marsh spot than applications of the salt to the soil. Heintze (1938) has published the results of her examination of marsh spot soils for readily soluble manganese and also the results of pot trials in which marsh spot was produced in peas grown in soil and in sand deficient in available manganese.

The symptoms of the disease, which have been described in some detail by de Bruijn (1933), are confined to the seed and are not visible until the pea is full size and at the stage when usually picked for

cooking. If at this stage the cotyledons of an affected pea are separated, one or more of the spots, having a water-soaked appearance, are seen on the inner surface of each, usually in a corresponding position. The cells of the affected area die and form a lesion involving more or less cotyledonary tissues (Fig. 1 A). The lesion may be entirely superficial or may form a pocket of brown or grey shrunken cells which, in very severe cases, is visible as a dark scar through the seed-coat of the unopened pea. Less frequently the plumule is necrosed, but no other part of the seed has been observed to be affected. Pods containing healthy seed are found on the same plant together with pods containing only diseased seed. Also, healthy and diseased peas may be found together in the same pod.

Whole peas from various sources have been analysed for manganese content by Lewis (1936), Löhnis (1936) and Heintze (1938). The present authors considered that additional light might be thrown on the problem of manganese in relation to marsh spot by determining the distribution of the element in the diseased pea. First, it was decided to compare the manganese content of necrosed and healthy cotyledonary tissue dissected from diseased peas drawn from a single sample grown on only one soil. It was found, however, that the amount of manganese was in both instances too low to produce a significant figure for the quantities of material available for analysis. Next, the distribution of manganese was determined among the various parts (cotyledon, germ and seed-coat) of affected seeds, and compared with corresponding parts of healthy seed of the same variety grown on soils which had never been known to produce marsh spot. The results of these investigations suggested that size of pea might influence the result of analysis of whole peas for manganese content, and this point was tested.

Samples of a single variety of pea, Harrison's Glory, were used throughout. This variety was especially selected because a severely diseased sample (Ref. No. 2C114) was available which was exceptionally suitable for dissection. All the peas of this sample had cotyledonary lesions which were unusually deep, and all the plumules were affected.[1] The size of sample provided sufficient necrosed cotyledonary tissue for analysis, but, as with other parts of the seed, the weight of tissue used for each determination and the number of determinations made was severely limited by the relatively small number of diseased peas in hand.

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[1] This sample was the most severely affected of the 743 field and plot samples examined in the survey made in 1933 and 1934 by Furneaux & Glasscock (1936), and was reported upon by the Official Seed Testing Station at Cambridge as "being more heavily affected than any we have previously seen".

Further, as the variety is widely grown, disease-free seeds from commercial crops grown on soils which had never been known to produce marsh spot were readily obtainable. Two such samples, grown at Folkingham and Lincoln Heath respectively, were supplied through the kind offices of a firm of seedsmen. These latter samples had been threshed and graded by the ordinary commercial process, so that there was little variation in size of the pea. Sample No. 2C114 had been picked and threshed by hand and had not been graded, but the year of growth (1934) was exceptionally good for the pea crop so that, although a greater number of small peas was present, it was otherwise as uniform as the commercial samples.

METHODS OF ANALYSIS

Before analysis, all samples were dried to constant weight in the steam oven. Manganese was estimated by the colorimetric method, oxidation to permanganate being carried out by the periodate method of Willard & Greathouse (1917).

For the estimation of whole peas, about 6 g. of the oven-dried peas were used for each analysis, and the procedure adopted was exactly as described by Richards (1930).

For the estimations in different parts of the pea seed, a different analytical technique was adopted because of the small number of seeds available in some samples. A rapid wet combustion, as described by Wain (1938), using a mixture of concentrated sulphuric, perchloric and nitric acids, was carried out on 0·5–2·0 g. of the dried material, the perchloric acid being driven off when the organic matter had been completely oxidized. The residue was diluted with water, boiled and filtered, the final volume of filtrate and washings being evaporated down to about 10 c.c. The colour was then developed and the solutions matched in the usual manner.

NO LOSS OF MANGANESE BY SOAKING

As a preliminary to satisfactory dissection of the pea seeds it was found necessary to soak them in distilled water for 24 hr. In order to make sure that no manganese was lost in the process, both soaked and unsoaked peas were analysed for comparison. One hundred and fifty whole peas of similar size were selected from the Lincoln Heath sample. Half of this number was soaked in distilled water for 24 hr. before drying in the steam oven. the remainder being untreated. Six determinations

were made in both soaked and unsoaked groups. The results are set out in Table 1.

Table I. *Manganese content of soaked and unsoaked seeds.*
Lincoln Heath sample

	Soaked. Manganese p.p.m.	Unsoaked. Manganese p.p.m.
	8·7	8·6
	9·0	8·5
	8·8	9·2
	8·4	8·7
	9·0	8·6
	9·1	8·8
Average	8·8	8·7

In the unsoaked seed the quantities of manganese range from 8·5 to 9·2 p.p.m. with an average of 8·7 p.p.m., and in the water-soaked peas from 8·4 to 9·1 p.p.m. with an average of 8·8 p.p.m. These figures strongly indicate that no manganese is lost during a short period of soaking—a result to be expected, since it is unlikely that stored substances would be lost during the absorption of water in the natural process of swelling prior to germination. Further, the small range of variation demonstrates the uniformity in the distribution of manganese among the sample groups selected for analysis.

DISTRIBUTION OF MANGANESE IN THE PEA SEED

The seed coat of the soaked pea was ruptured by scratching with a mounted needle, and slipped off by exerting pressure between the thumb and forefinger. The cotyledons were then readily separated, and a cut was made through the centre of the brown patch on each flat inner surface, thus exposing the pocket of necrosed tissue, part of which was removed with a scalpel (Fig. 1 B). A portion of the adjacent unaffected cotyledonary tissue was cut out in the same way (Fig. 1 B), and healthy and diseased tissue derived from a number of seeds analysed separately. In removing portions of tissue in this manner from the centre of the cotyledon, care was taken not to include any of the peripheral tissues of the outer convex surface, which were peeled off and analysed separately (Fig. 1 C). These latter tissues included the epidermis, together with several layers of underlying cells, but, as the number of layers was variable, the figures obtained in analysis are not suitable for close comparison. The germ, which comprises plumule and radicle, usually

remained attached to one of the separated cotyledons, from which it was removed by the point of a scalpel.

Except for the absence of necrosed cotyledonary tissue in the healthy peas, the method of dissection was the same in the diseased and healthy seed.
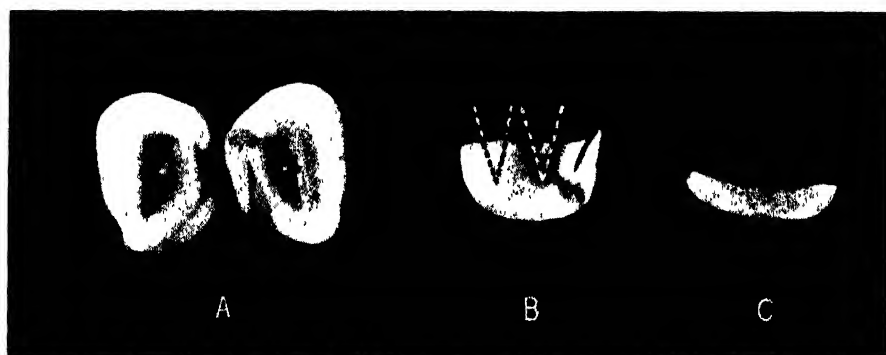
Fig. 1. Dissection of diseased pea seed. A. Separated cotyledons showing lesion in centre of each. B. Part of cotyledon. Dotted lines indicate portions of healthy and of necrosed tissue removed for analysis. C. Peripheral tissues as removed for analysis. All × 3.

The amounts of manganese found in the different parts of the diseased seed from Romney Marsh and the healthy seed from Folkingham are set out in Table II.

Table II. *Distribution of manganese in healthy and diseased seeds*

Diseased sample (2C114)		Healthy sample (Folkingham)	
Part of seed	Manganese p.p.m.	Part of seed	Manganese p.p.m.
Cotyledon: Outer tissues	5	Germ	15
Germ	3	Cotyledon: Outer tissues	11
Seed coat	2	Centre tissues	6
Cotyledon:		Seed coat	4
Centre tissues· (a) Normal	<2		
(b) Necrosed	< 2		

Referring to the diseased sample, it was found that both normal and necrosed tissue from the centre of the cotyledon contained only a trace of manganese. The colour which developed in the estimation was in either case hardly discernible, but calculated on the weight taken is less than 2 p.p.m. of oven-dried material. The highest figure, 5 p.p.m., is given for the outer layers of the cotyledon. The amount of manganese in the germ and the seed-coat is relatively low, being 3 p.p.m. and 2 p.p.m., respectively.

It is evident that all parts of the seed from the Folkingham sample are richer in manganese than the corresponding parts of the diseased seed. The order of distribution is different, notably in that the tissue from the centre of the cotyledon with 6 p.p.m. contains a greater concentration than the seed-coat with 4 p.p.m. and the germ with 15 p.p.m. contains a greater concentration of manganese than the outer layers of the cotyledon with 11 p.p.m.

MANGANESE CONTENT IN RELATION TO SIZE OF PEA

The richness in manganese of the outer tissues of the seed, as compared with the centre, is outstanding in the diseased sample and is evident to a less marked extent in the healthy sample. The shape of the soaked seed of the variety on which analyses were carried out is subspherical, and it is clear that, the smaller the size of the pea, the larger its outer surface in proportion to its total volume. It was thought possible, therefore, that the small peas of a sample might have a higher manganese content per unit weight than the large peas. To test this point, a quantity of the largest and of the smallest peas were selected by eye from the diseased and healthy samples, and each group was analysed separately. Each determination was made on 20–30 peas. The results, which are set out in Table III, show that there is a marked uniformity of manganese content within each group, but, contrary to expectation, in the diseased sample a given weight of small peas (oven-dried) proved to contain less manganese than the same weight of large peas. Thus, the average of six determinations made on the small peas is 3·4 p.p.m., while the average for five determinations made on the large peas is 4·1 p.p.m., giving a preponderance of 0·7 p.p.m. in the latter. In the Lincoln Heath sample, however, the average of seven determinations gives a difference of 0·6 p.p.m. in favour of the small peas.

Table III. *Manganese content of large and small seeds*

Diseased sample (2C114)		Healthy sample (Lincoln Heath)	
Large Manganese p.p.m.	Small Manganese p.p.m.	Large Manganese p.p.m.	Small Manganese p.p.m.
--		8·5	9·5
4·2	—	8·4	9·4
4·3	3·3	8·3	8·4
4·0	3·5	8·6	8·8
4·0	3·1	9·3	9·9
4·1	3·4	8·8	9·5
4·1	3·5	8·8	9·4
Average 4·1	3·4	8·7	9·3

DISCUSSION

Heintze (1938) has shown that readily soluble manganese is low in soils which produce marsh spot in pea crops. It has also been demonstrated by Löhnis (1936) and Lewis (1936) that the affected peas are lower in manganese than the unaffected peas drawn from the same sample, and that the manganese level in these unaffected peas is usually lower than that of peas of the same variety drawn from samples which are completely free from the disease. The figures given by Lewis (1936) show that, with many samples, the manganese content of the affected seed is only two-thirds or one-half the content of the unaffected seed, even though the sample represents a single variety which has been collected from a crop grown on a single soil type as determined in the survey made by Furneaux & Glasscock (1936). It is somewhat surprising that such large differences in manganese content should exist, for not only is the whole crop grown under similar conditions on a single soil, but it has been established that healthy and diseased peas are to be found in the same pod without any apparent special arrangement with regard to position, and pods containing diseased peas are found on the same plant together with pods containing only healthy peas.

In his microscopic examination of peas affected by marsh spot, Grieve (1934) has shown that the cytoplasm disappears from the necrotic cells, leaving the dry starch grains. It seems likely, therefore, that any substances, including those containing manganese, which are present in the cytoplasm of the affected cotyledonary cells would also migrate from the diseased area. On this account, diseased peas might be expected to contain less of such substances than healthy peas of the same sample.

Sample No. 2C114 contained no healthy peas for comparison with the diseased specimens, and the amount of manganese in both necrosed and healthy tissue of the cotyledon was negligible so that only very slight quantities could have been lost with the cytoplasm. It must be stressed, however, that the manganese content of this sample was very low indeed, being the lowest of the numerous samples analysed by Lewis. That low manganese content is not a character of the variety is demonstrated by the fact that other diseased samples of Harrison's Glory were not proved to be notably low. The seed from which No. 2C114 was grown, for example, and of which 15 % were affected with marsh spot, proved on analysis by Lewis to contain 15 p.p.m. in the healthy seed and 8 p.p.m. in the diseased. The lower figure approximates that found for the healthy sample grown at Lincoln Heath in which the central

cotyledonary tissue contained 6 p.p.m. From this it appears that where the level of manganese in the starch-containing cotyledonary tissue is not unusually low relative to that in other tissues, the bulk of the manganese in the seed is resident in that tissue. If necrotic pockets are formed, it is possible that the migration of cell contents will reduce the total manganese of the pea which analysis would prove to contain less than a healthy pea of similar size from the same sample. It is not supposed that a disease caused by the deficiency of a substance necessarily manifests itself by showing less of that substance in the tissues in which the symptoms appear than in adjacent healthy tissue, but it is interesting to note from the figures of the analysis of sample No. 20114 that tissue at the centre of the cotyledon can remain apparently healthy with only minute traces of manganese present.

It has been pointed out by de Bruijn (1933), and confirmed by Löhnis (1936) and Furneaux & Glasscock (1936) that the heavier and larger peas of a sample are more prone to marsh spot than the others. Thus, in dividing a sample into two groups, healthy and diseased, there must be a tendency for the individuals of the former group to be smaller in size than those of the latter. In the present investigation, peas graded into large and small sizes showed considerable uniformity in manganese level within each size group, but significant differences were found to exist between the groups. This suggests that peas of uniform size should be selected for analysis when the relative manganese levels of two or more samples are to be tested.

SUMMARY

1. An outline of recent investigations on the cause of marsh spot in pea seeds indicates that the disease is caused by a deficiency of available manganese in the soil.

2. The symptoms of the disease are very briefly described.

3. The methods of analysis used by the writers for determining the amounts of manganese in whole peas and in different parts of peas are described.

4. As no loss of manganese was found to result from soaking the peas in water for 24 hr., soaked peas were used for dissection in preference to dry peas.

5. Referring to the diseased peas, the highest level of manganese was found in the peripheral tissues of the cotyledons, followed by the germ and seed-coat. Only slight traces of manganese were found in the healthy

and in the necrotic tissue from the centre of the cotyledons. All parts of the healthy seed were richer in manganese than the corresponding parts of the diseased sample. In addition, the order of distribution was different; notably in that the tissue from the centre of the cotyledon contained a higher level than the seed-coat, and the germ a higher level than the outer layers of the cotyledon.

6. A given weight of small peas proved to contain less manganese than the same weight of large peas selected from the diseased sample. The reverse was found to be true for similar size groups selected from the healthy sample. These differences in the manganese content of size groups suggest that peas of uniform size should be selected for analysis when the relative manganese levels of different samples are to be tested.

7. It is suggested that migration of cell contents from the necrotic tissue of diseased peas may partly account for the differences in manganese content of healthy and diseased peas.

REFERENCES

DE BRUIJN, H. L. G. (1933). *Tijdschr. PlZiekt.* **39.** 281.
FURNEAUX, B. S. & GLASSCOCK, H. H. (1936). *J. agric. Sci.* **26,** 59.
GRIEVE, B. J. (1934). *Ann. appl. Biol.* **21,** 636.
HEINTZE, S. G. (1938). *J. agric. Sci.* **28,** 175.
LACEY, M. S. (1934). *Ann. appl. Biol.* **21,** 621.
LEWIS, A. H. (1936). *In litt.*
—— (1939). *Emp. J. exp. Agric.* **7,** 150.
LÖHNIS, M. P. (1936). *Tijdschr. PlZiekt.* **42,** 159.
OVINGE, A. (1935). *Landbouwk. Tijdschr., 's Grav.,* **47,** 375.
—— (1938). *Tijdschr. PlZiekt.* **44.** 208.
PETHYBRIDGE, G. H. (1936). *J. Minist. Agric.* **43,** 55.
RICHARDS, M. B. (1930). *Analyst,* **55,** 554.
WAIN, R. L. (1938). *J. S.-E. agric. Coll. Wye,* **42,** 146.
WILLARD, H. H. & GREATHOUSE, L. H. (1917). *J. Amer. chem. Soc.* **39,** 2366.

STUDIES ON THE METABOLISM OF FOWLS

II. THE EFFECT OF ACTIVITY ON METABOLISM

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(With Three Text-figures)

INTRODUCTION

WHILE the immediate object of the work to be described was to secure data on the comparative energy values of Sussex ground oats and white maize meal for fowls, a preliminary investigation of the effect of visible activity and diurnal rhythm on the observed metabolism has yielded additional results of no small value.

Before discussing these it seems worth while digressing for a moment to mention the advantages of the direct over the indirect method when working with adult fowls.

Mitchell *et al.* (1927) found with Plymouth Rock cockerels no less than eleven out of thirty-two giving R.Q.'s <0·70 going as low as 0·60, and six out of thirty-one in the pullets, while four out of six Rhode Island Reds were in this category. Nichita & Mircea (1933) found low R.Q.'s down to 0·537 in most cases with fasting bantam and Transylvania birds. Dukes (1937) found twenty-eight low R.Q.'s out of 156.

Now although there are formulae and theories such as, for example, Bleibtreu's equation, enabling corrections to be made in certain cases, chiefly in human subjects, the most usual procedure with birds seems to be either to reject such observations out of hand or, alternatively, to assume that all R.Q.'s <0·707 are really equal to 0·707. Neither of these procedures can be considered scientifically satisfactory. On the other hand, one can hardly advocate the use of corrections which, in human beings, depend on empirically determined constants, to birds, without further investigation, more especially where a not inconsiderable extrapolation is involved.

Barott *et al.* (1938) have pointed out only a few months ago that experimenters have quite unjustifiably adopted the R.Q. of protein metabolism for mammals (=0·801) in work on birds, whereas, according to their

computations based on the heat of combustion of uric acid, and Colman & Hughes's figures for the composition of hen's urine, this should be 0·705. The use of the mammalian figure for protein would clearly lower the non-protein R.Q., but the total R.Q. would be unaffected. There is clearly much to be discovered about the avian metabolism before indirect methods can be considered fully satisfactory for calorimetric work with birds.

Both Barott *et al.* and Mitchell, found normal R.Q.'s when working with *chicks*.

To return to the question of the effect of activity. Nearly all workers with fowls, including Mitchell, Nichita and Barott, have found a very considerable diurnal variation of metabolism which complicates work considerably. How great this effect may be is well shown by the curves, hitherto unpublished, of Fig. 1. These were obtained some twelve years ago by one of the writers (T. D.) working with Light Sussex cockerels placed in the small pig calorimeter in groups of six at a time. Each bird was enclosed in a separate cage. The discussion of the time variation in this case is rendered difficult by the fact that a part of the rhythm observed is clearly due to a rhythmic variation of activity within the same or similar time limits.

The matter of a diurnal rhythm of metabolism has been specifically investigated by Mitchell *et al.* (1927) and also by Benedict and his collaborators (1932). Both actually found some evidence of a difference between day and night metabolism, but the first-mentioned investigators are inclined to reject their evidence (*a*) because the difference appeared too great to be due to such a cause by analogy with man, and (*b*) because they had expected the maximum to coincide in time with that of man in the afternoon.

Benedict *et al.* (1932) are also inclined to doubt the reality of the differences they find on the score that "the activity records...are only of partial value in indicating the true muscular tonus which...results in a higher metabolism". While this may well be so, this sort of activity is not what is usually meant by the term; and it is worthy of note that Nichita & Mircea found the difference in metabolism to persist right up to the point of death by starvation, although the birds remained in a passive moribund condition for several days. Probably only some activity of a rather fundamental kind, such as that envisaged by Benedict, could continue to manifest its effects under such conditions.

An interesting memoir on diurnal rhythms in general has recently been published by Brody (1938).

In the experiments described in this paper we have tried to control, or correct for, the visible activity of the bird, and so to find out whether there is any diurnal rhythm of metabolism when the results are not complicated by visible activity. It would seem that any diurnal rhythm, which persists at temperatures above the critical, when the effect of visible activity is controlled, must be due to changes in muscular tonus, to some rhythm in the activity of the endocrinal organs or to some other factor affecting the heat-regulating centre.

The birds used in the following experiments were all of the Light Sussex breed, some from the University Farm, Cambridge, and others from Messrs Chivers of Histon.

They were fed on a maintenance ration of pellets of the following composition computed according to weight at the rate of 25 g. per day per kg. live weight:

Birds A and B			Birds C–J		
Bran	10	parts	Maize meal	25·2	parts
White maize meal	35	,,	Weatings	33·6	,,
Weatings	20	,,	Bran	16·8	,,
Sussex ground oats	7	,,	Sussex ground oats	12·6	,,
Wheat meal	25	,,	Fish meal	8·7	,,
CaCO₃	2·5	,,	Cod-liver oil	1·3	,,
NaCl	0·5	,,	Mineral mixture	1·8	,,
Casein	5	,,			
Dried yeast	1·5 g./day				
Cod-liver oil	1·4 g./day				

Birds A and B

A set of preliminary experiments with birds A and B showed that observations taken at ten-minute intervals of time would afford but an imperfect picture of the effect of activity on metabolism. The technique of these experiments was practically identical with that employed in the later, more important experiments on birds C–J.

The results obtained in these experiments showed:

(*a*) That an experimental period of 1½ hr., allowing 1 hr. observation, was barely sufficient to yield enough figures from which to calculate a trustworthy average.

(*b*) That on a maintenance ration there were significant variations in the metabolism which were correlated with the time of day.

The results of these preliminary tests are given in Table 1 for the fasting periods. As far as they go it will be observed that they are in general agreement with those shown in Fig. 1 for the groups of six fowls

tested together. It will be noticed that in both birds the *fasting* level in the second fasting period is lower than that in the first. This would appear to show that the 1 day's *maintenance* feeding which they were given between the two did not suffice to offset entirely the 48 hr. fast which they had undergone. On the other hand, the group of fowls shown with round dots in Fig. 1 did re-attain their previous level of metabolism when *recrammed* after a 48 hr. fast.

Results obtained when maintenance and supermaintenance rations were fed to these birds were unsatisfactory, more than half of the super-maintenance results were lost entirely owing to lack of sufficient control of the activity of the bird, and are omitted.

Table I. *Average sitting metabolism of birds A and B*

	Bird A				Bird B		
Exp.	Time*	Meta-bolism	Hr. from beginning of fast	Exp.	Time	Meta-bolism	Hr. from beginning of fast
First fasting period:							
	12.10–13.30	182·9	25	5	11.20–12.50	164·2	26
2	16.0 –17 20	–	29	6	15.25–16.50	160·0	30
3	23.50– 1.20	155·8	37	7	23.35– 1·0	118·6	38
4	5.20– 6.50	157·2	43	8	5.35–6.45	137·7	44
Second fasting period:							
9	11.20–12.50	157·0	25	13	11.20–12.50	150·9	27
10	15 40–17.10	175 4	29	14	15.25–16.50	139·8	31
11	23.40– 1.0	140·0	37	15	23.35– 0.55	123·3	39
12	5.20– 6.50	136·9	43	16	5.40– 7.0	115·2	45

* Times are recorded on the 24 hr. system.

In the experiments which follow, for which birds C–J were used, the following technique was employed. The bird selected was put into the experimental chamber and kept under observation for a period of up to 3 hr. duration. The room and apparatus had been brought into equilibrium previously at a temperature above the critical, usually in the neighbour-hood of 25° C. No restriction was placed upon the bird's movements, apart from that inherent in such confinement, except as noted in particular cases. The cage is large enough to permit of the birds standing up if they wish. Immediately after the insertion of the bird in the chamber, the heat and water-vapour compensator in the balancing chamber were put into operation; and the main observations were begun after the lapse of half an hour which previous tests had shown to be sufficient. At the close of an experiment the water-vapour content of the chambers was taken with a chemical hygrometer as a check on the performance of the hair hygrometers used for regulation.
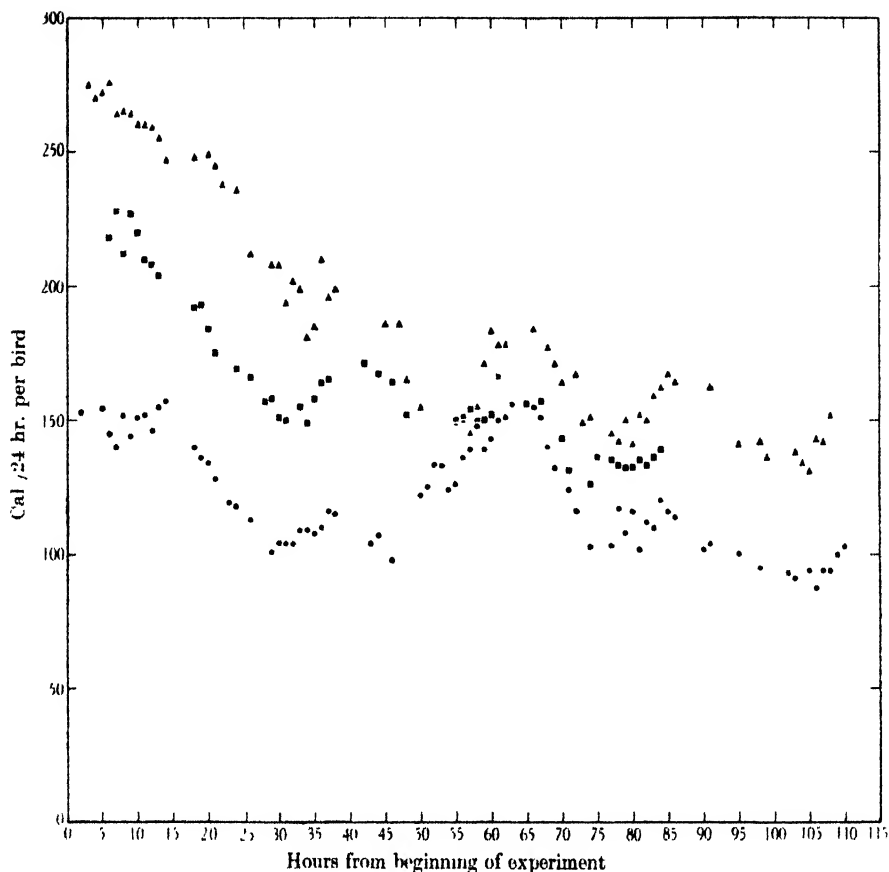
Fig. 1. Metabolism of Light Sussex cockerels after cramming, deduced from the total heat output of six such birds placed in the smaller pig calorimeter. Huddling was prevented by enclosing each bird in a separate cage.

● Observations on six birds, average weight 2330 g., crammed with an average of 91 g. of a mash consisting of 13 parts Sussex ground oats, 3 parts dried milk and 18 parts of water (total dry matter 42·8%). After 48 hr. the birds were removed from the calorimeter, recrammed with an average of 156 g. of the above mash (total dry matter 42·3%) and immediately replaced in the instrument (8–13 August 1927).

■ Observations on six birds, average weight 2717 g., crammed with an average of about 145 g. of the above mash (precise amount doubtful owing to accident in cramming) (dry matter 44·8%) (1–5 November 1927).

▲ Observations on six birds, average weight 2892 g., crammed with an average of 132 g. of the above mash on top of free feeding up to the moment of cramming (dry matter 44·8%) (14–19 November 1927).

Birds C and D

Birds C and D were used in an only partially successful attempt to separate the diurnal rhythm of metabolism from diurnal changes in the visible activity. The technique varied somewhat in the different tests as follows.

Exp. 1. Bird C. Fourteen tests of 1½ hr. each (including preliminary period) extending over two nights and a day. Bird fasted from beginning to end of experiment. Metabolism readings every 5 min. Activity recorded for ½-1 min. before each metabolism observation either by a notation system or by a written description. Periods of standing, shuffling or when the bird was asleep with its head under its wing were excluded.

Exp. 2. Bird D. Tests of 2 hr. each (including preliminary period) beginning 11.15 a.m., 4.30 p.m. and 9.30 p.m. on one day and 10.45 a.m. the day after. Bird fasted from 24 hr. before the beginning until the end of the experiment. Metabolism observations every 5 min. Activity observations by notation for 1 min. before metabolism readings. Periods of standing and shuffling excluded. Sleep, with head under wing included, as most of night period spent thus.

Exp. 3. Bird C. Tests of 2 hr. each (including preliminary period) beginning 10.30 a.m. and 4.30 p.m. one day and 10.30 next morning. Bird fasted from 24 hr. before beginning until the end of the experiment. Metabolism noted whenever this changed. Activity record continuous by notation. Periods of standing and shuffling excluded. Sleep, with head under wing, included.

Table II gives the results of these experiments. The rhythm of metabolism is expressed as the percentage excess of the morning over the night periods (morning over afternoon in Exp. 3). It can be seen that the birds were more than twice as active during the morning as in the afternoon and night periods, so that no certain conclusion can be drawn from these results as to whether the diurnal rhythm of metabolism observed by us and other workers is caused *entirely* by differences in visible activity or whether some more fundamental phenomenon is also involved.

Table II. *Metabolic rhythm of birds C and D*

Exp.	Metabolism % excess	Mean activity (points)	Activity % excess (points)
1	42·0	90	100
2	13·3	42	55
3	13 4	65	77

The system of recording activity continuously by notation proved very satisfactory and better than any mechanical device, several of which were tried, including photography at intervals of a few seconds; but it was found that small differences in the head and neck movements

could have a considerable effect on the metabolism, and these activities could not be controlled satisfactorily.

Birds E–J

We next, therefore, made a rather elaborate attempt to control the activity of the birds so that we could obtain, artificially, periods of equal activity during the day and the night, within the limits of accuracy of the system of recording by notation. Such differences of activity as remained, and they were in some cases considerable, we have tried to remove by a statistical method.

The activity was controlled in the following way. During the morning period, when the activity was normally at its peak value, we allowed the bird to move without restraint, while in the evening and night periods the bird was stimulated from time to time with a motor horn and a mechanical stimulator placed in the calorimeter. In this way we attempted to reproduce during the evening and night periods an activity comparable with that exhibited during the morning. Continuous observations of the activity were made:

(a) of movements of the head and neck by the system of notation used in the preceding experiments and more fully described in the section on the statistical computation;

(b) of the position of the head and neck, also classified;

(c) in some cases of the amount of time the bird spent in sleep, judged by whether its eyes were open or closed.

Five birds were used for this experiment, E, F, G, H and J. The experiments on E, F and G lasted for 2 days and consisted of six tests of 2 hr. duration (including the preliminary half-hour) beginning at 10 a.m., 5 p.m. and 10 p.m. on each day. The birds were fasted for 24 hr. before the start of the experiment. The experiment with bird H lasted for 4 days and was conducted in the same manner, while that on bird J lasted for 3 days beginning with a night period and ending with a morning period, that is, seven tests in all with this bird. Measurements of the metabolism were made whenever it changed, and the means of these observations, weighted for the time during which each figure was maintained, were used in computing the average metabolism of each test. For the direct comparison, without statistical analysis, we omitted periods of standing, shuffling and when the bird was asleep with its head under its wing, but not periods of sleep in the normal sitting position. There was little difference in the amount of experimental time excluded under these heads at different times of day, except that the periods of

sleep with head under wing were rather greater in the afternoon and morning periods.

A definite fall in the mean level of metabolism was noted on succeeding days and is mentioned in more detail in the statistical section.

The diurnal rhythm of metabolism has been computed in three different ways:

(i) Over the first 2 days, taking the trend of metabolism mentioned above as linear.

(ii) Over the first 2 days, taking the general trend of metabolism by a freehand, quasi-exponential curve.

(iii) Over the whole experiment where it continued for more than 2 days, representing the general trend of metabolism by a freehand curve as in (ii).

The results of these computations are given in Tables III and IV, in which the diurnal rhythm of metabolism between morning and night periods and between afternoon and night periods is calculated as a percentage of the night value. It will be seen that the activity is very nearly the same in the different periods, the residual difference corresponding to four or five small movements of the head per minute between the morning and night periods and about two such movements between

Table III. *Diurnal rhythm of metabolism between morning and night periods*

Bird	Metabolic rhythm %			Mean activity 1st two days	Difference Morn.– night	Mean activity Whole exp.	Difference Morn.– night
	1st method	2nd method	3rd method				
E	16·1	15·6	—	71·8	9·4	---	·
F	9·9	6·7	—	35·0	0·4	—	—
G	9·5	8·8	—	28·7	3·9	—	—
H	12·7	8·6	6·0	28·4	7·7	29·4	5·4
J	8·3	7·3	5·9	30·9	2·3	29·9	2·9
Mean	11·3	9·4	--	39·0	4·7	—	

Table IV. *Diurnal rhythm of metabolism between afternoon and night periods*

Bird	Metabolic rhythm %			Mean activity 1st two days	Difference Aft.– night	Mean activity Whole exp.	Difference Aft.– night
	1st method	2nd method	3rd method				
E	10·0	9·7	—	71·6	9·1	—	---
F	3·1	1·8	·	34·1	−1·3	—	—
G	−4·9	−3·8	—	27·6	1·5	--	—
H	3·0	1·5	0·4	24·8	0·4	26·1	−1·3
J	5·5	3·5	1·8	29·9	0·2	29·2	1·6
Mean	3·3	2·5	—	37·6	2·0	—	—

the afternoon and night periods. The position of the head was strongly correlated with the amount of visible activity, since the bird took up an alert position when the visible activity was large and vice versa. The time of sleeping, where recorded, tended to be somewhat less in the night periods than in the morning ones, and rather greater in the afternoons. This was no doubt an effect of the stimulation, and it was clear that difficulties would have arisen in the calculations on this account had any attempt been made to push the stimulation further to obtain exactly equal activities at night and in the mornings.

It should be noted that it is plain from the subsequent statistical work that the small remaining activity differences would make very little difference to the figures for the metabolic rhythm. It is clear therefore that there is a residue of diurnal metabolic rhythm even when the activity is very carefully controlled amounting to from 8·6 to 11·3 %, according to the method of calculation, for the night and morning periods and 2·0–3·3 % for the afternoon periods. The results of the experiments on different birds are, moreover, in close agreement with one another.

Statistical investigation

For the statistical investigation bird D was included as well as E, F, G, H and J. Periods of standing were excluded but all other periods were included.

Since the metabolism is liable to vary from causes other than muscular movement it was decided to compare the *change* of rate of metabolism which follows immediately on *change* in activity with that change in activity itself. In Fig. 2 change of metabolism is plotted against change of activity for some 280 selected periods of about 15 min. duration, in which other causes of variation of metabolism would presumably have little time to make themselves felt and consequently would not affect the results to any great extent. From the examination of Fig. 2 it is clear that there are two distributions intersecting at an angle—hence the dumb-bell shape of the scatter diagram. An examination of the data showed that the steeper distribution was almost entirely due to the inclusion of data from birds F and G. Separate correlation tables and regression equations were therefore computed for these birds.

The final equations were as follows: If D is the deduction to be made from the observed rate of metabolism to reduce it to the basis of zero activity, and A is the activity score:
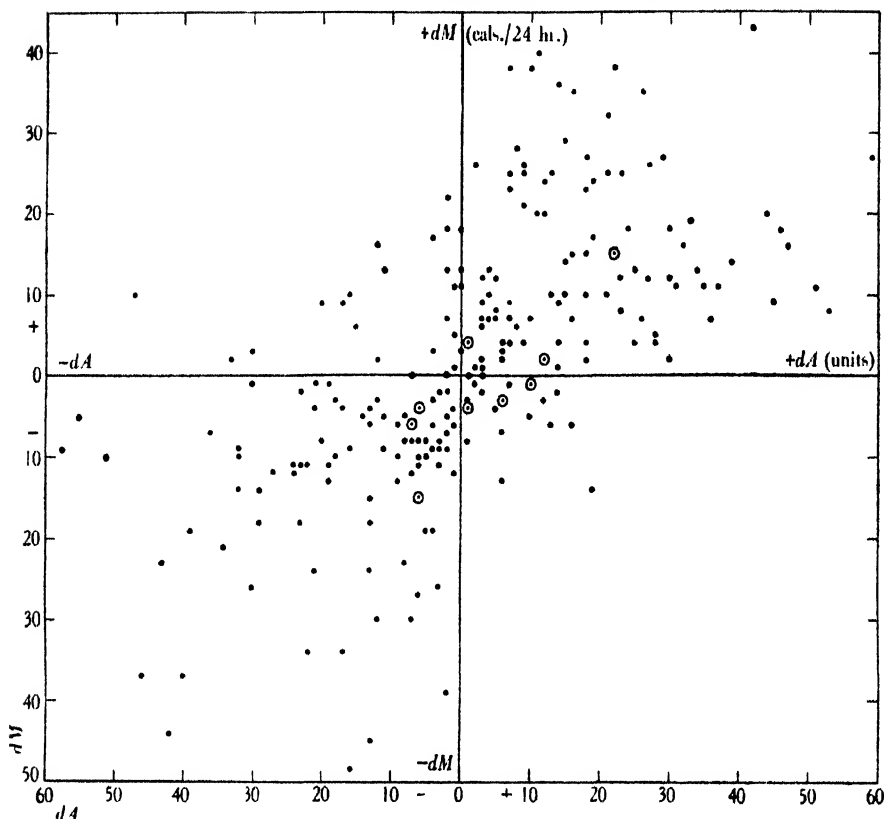
Fig. 2. Scatter diagram of observations of change of rate of metabolism with change of
activity. The *dA* axis shows change of activity in the units selected and the *dM*
axis the corresponding change of rate of metabolism in cal./24 hr.
 ⊙ indicates two identical observations.

For birds D, E, H and J

$$D = 0.395A + 1.6 \text{ cal.}/24 \text{ hrs.}$$

For birds F and G

$$D = 1.35A - 0.7 \text{ cal.}/24 \text{ hrs.}$$

In these computations only the movements of the head and neck
pecks and shuffles were considered, and zero activity was considered to
be that exhibited when the bird was asleep with its head under its wing,
the waking immobile position being counted at 20 points for A.

Hence for a period of 15 min. in which 2 shuffles, 10 pecks, 4 large,
13 medium and 30 small movements of the head and neck had been
recorded, the bird being awake all the time, the average activity score
would be—on the system adopted—

$$20 + \frac{(2 \times 20) + (10 \times 6) + (4 \times 4) + (13 \times 2) + (30 \times 1)}{15} \text{ points.}$$

The requisite data were obtained by visual observation by an observer giving his whole attention to the work; but there was even then inevitably a certain amount of error due largely to incorrect classification and to errors in counting when movements are rapid (as in shaking the head). The correlation between change in metabolism and change in activity was nevertheless closer than was anticipated amounting to $r = 0.61$ for birds D, E, H and J and to $r = 0.79$ for birds F and G.

As explained above a fall in the average metabolism in the second of two successive quarter hours in which the average activities had been, for example, 60 and 25, was taken as being due *entirely* to the fall in the
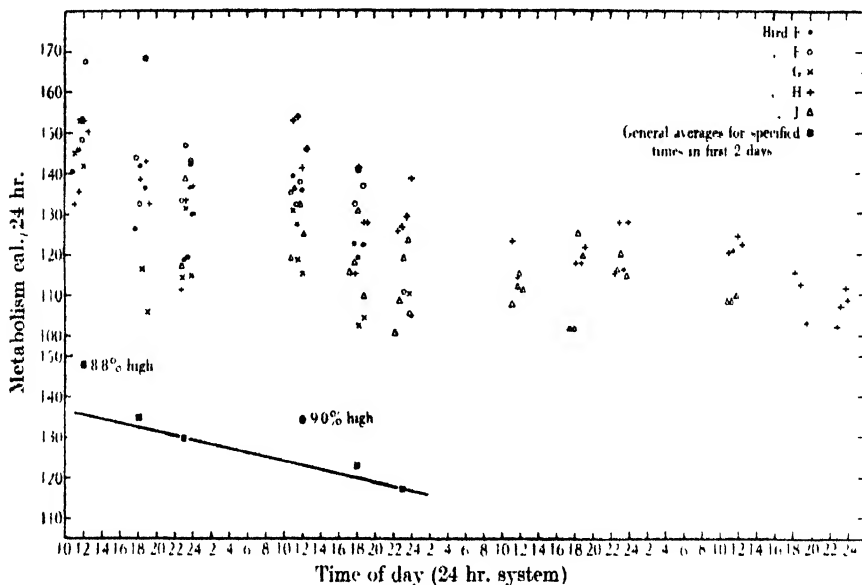
Fig. 3. Metabolism of cockerels, grouped according to time of day when the observation was made and corrected for activity.

activity. For the reason stated above and in view of the large number of comparisons available and plotted in Fig. 2 it was felt that such an assumption was justified.

By means of the above equations it is possible to correct the observed sitting metabolism of the fowls for the effects of activity. This has been done, dividing the time of observation into half-hour periods, and the results are shown in Fig. 3. The wide scatter of the points in each of the morning, evening and night observations, corresponding to approximately 12 noon, 6 p.m. and 11 p.m., is very noticeable, but not unexpected, as, apart from small experimental errors, both the normal individual differences between the birds and the probable error involved

in using the regression equations (± 12 cal./24 hr.) are included in the data as plotted. A trial plotting of the uncorrected observations in the same way showed two to three times the scatter.

The points lower down on the diagram show the result of averaging all the morning, evening and night observations on five fowls for the first 2 days of fast. This process is not carried beyond the second fasting day since, as will be observed, only two birds were fasted beyond this point and the observations are not numerous. Allowing for this, the trend is not flagrantly at variance with the result for the first 2 days.

It will be observed that there is a definite fall in the mean level of metabolism from the first to the second day which is in accordance with what we found in the preliminary work quoted in Table I, and with the results obtained 12 years ago shown in Fig. 1. It is of course to be expected and has been observed previously by Nichita & Mircea (1933), Benedict *et al.* (1932) and others in the domestic fowl. Breirem (1936) found it to continue in the pig for as long as 10 days from the beginning of the fast, and it has been discussed at some length by one of the present authors (Deighton, 1929), who considers that it cannot be accounted for by the presence of residual food in the alimentary tract.

Apart from this more or less continuous fall there appears to be a definite rhythm of metabolism amounting to 8.9%. This rhythm is calculated as the mean percentage rise of the metabolism in the morning period, reduced to zero activity, over the mean metabolism in the night period also reduced to zero activity allowing in each case for the previously mentioned continuous fall and assuming, for this purpose, that this fall is linear. It corresponds closely to the first method of computation used in the previous discussion for which the result was 11.3%. The difference between the results corresponds to residual differences in activity in the first method and error residue in the second.

These figures confirm those obtained by Barott *et al.* (1938) who found a variation of approximately the same amount in young male chicks about 120 days old. In their experiments activity was not actually excluded, although reduced by placing the birds in cages to fit them, while differences in activity between birds was presumably evened out, as they used several birds at a time. Under these circumstances the daily variation in metabolism has a chance to show itself, and the *uniformity* of this variation in the results of these experimenters is very remarkable. It is not possible from our results to confirm the times of maximum and minimum found by Barott and his collaborators, namely 8 a.m. and 8 p.m., as our experiments were performed before the appearance of their paper.

According to them the 6 p.m. and 11 p.m. metabolism are equal; ours seem to show a slightly higher figure at 6 p.m.

Mitchell *et al.* (1927), as has been stated, were inclined to reject what evidence they found for a diurnal rhythm on the score that it was greater than might be expected and appeared at the *wrong time* by analogy with human beings. There is, however, no reason to suppose that the avian metabolism will necessarily agree with the human in this matter. We have evidence from our photoelectric cell records (see previous Paper I of this series), and from many personal observations during calorimeter tests, that the birds become active about the time of cock-crow, from 2 to 3 a.m. G.M.T., and become somnolent at about 4 p.m. G.M.T., almost irrespective of the time of year. The diurnal rhythm of their activity is thus quite out of step with that of human beings, and it is natural that their metabolic rhythm should follow this. We consider that there is now a sufficient amount of evidence accumulated to justify a belief in the existence of this diurnal rhythm of metabolism in fowls irrespective of the visible activity displayed but no doubt dependent on the general tonus of the muscles.

Attention has been called recently to the practical importance of determining the energy quota for the various activities of animals (*Report*, 1935) in order to arrive at more accurate figures for their energy requirements under practical farming conditions. The examination of the heat production from minute to minute by the balance calorimeter has afforded valuable information in this connexion. It appears that during standing the metabolism of the fowl is raised to a considerably greater extent than is usual in pigs and other quadrupeds, and even as compared with the 16 % difference found for human beings by Tepper & Hellebrandt (1938). From upwards of thirty cases examined in which the fowl remained standing sufficiently long to enable an estimate of its metabolism in the standing position to be made, it was found that this was on the average 42·0 % above the sitting level of heat evolution observed immediately before and after standing. The standard error of this mean was ± 2·42 % and the coefficient of variation 5·65 %. Limiting the survey to twenty-two fasting observations the average increase was 45·0 %—not greatly different from the above.

At the moment of rising to the standing position there is always, as might be expected, and as is found in all similar cases, a sudden efflux of heat due to the mechanical and physiological work done in raising the body, and this, in these birds, was very much greater than is usual in quadrupeds, sometimes amounting momentarily to more than 200 %

of the previous and subsequent sitting metabolism. Møllgaard (1923) considers that there is a compensating effect between standing meta- bolism and lying metabolism in the cow, such that, over a long period, the percentage of time standing does not affect the average metabolism appreciably. He does not, therefore, correct his metabolism figures for standing as Forbes does. The results of the present experiments are not such as to permit of this point being adequately discussed. It seems reasonable to suppose that much of this sudden liberation of heat may be due to the liberation of hot air from between the feathers, but if any abnormal amount comes from this source a considerable lowering of the sitting value should, one would think, be noted when the fowl sits down again. Some such lowering is frequently observed but this is never of anything like the same order of magnitude as the rise. If, however, the bird has had time to build up its "hot air reserve" while standing, this expected lowering of heat output would not necessarily take place.

A statistical survey of these results, taking fasting observations only, numbering 81 in all, was kindly made for us by Mr C. A. B. Smith, afterwards corrected from revised data by Dr J. Wishart, to discover whether any difference existed in this matter between individual birds and also whether the time of day had any effect. Dr Wishart concludes that this increase in metabolism on rising does not depend significantly upon the individual bird or upon time of day. It also appears to be independent of the actual level of the sitting metabolism.

From the practical point of view this high heat evolution on rising to the standing posture might be of some importance, since the amount of energy used by the bird in a day seems likely to be affected con- siderably by the number of times it gets up and sits down. Our birds, which were kept in cages in the laboratory, performed this movement very frequently at times, as our automatic records with the photoelectric cells show. On the open range it may well be that there is less of this type of movement, the bird taking its exercise by wandering about seeking food and grit.

A careful examination of our data on the above point, taking into account the time during which this large heat evolution takes place, shows, rather surprisingly, that the net effect averaged out over the 24 hr. is far less than might be anticipated. Thus experiments showed that the momentary rise of heat production on standing is equivalent to a period of about 15 sec. at peak value while this is itself, on the average, 98·5 % above the sitting value. From our photoelectric cell records we find that the birds rose from a sitting to a standing position some 36 times

in the course of 24 hr. From these figures it is easy to compute that the total increase in the average metabolism over 24 hr. due to this cause is only 0·62 %. Short periods are frequently encountered, however, in which this action is performed once or twice a minute and during this time the metabolism may be appreciably raised.

With regard to the times during which the bird remains standing the case is far otherwise. A calculation from our charts for 89 days showed that on an average the birds stood for $12\frac{3}{4}$ hr. out of the 24. Remembering that the percentage increase in metabolism associated with this position is 45 % it is clear that the feed will have to contain energy for approximately 24 % above the calorific equivalent of the sitting metabolism in order to cover this, if we may assume that the same time would be spent standing when on the range.

Finally, although we cannot adduce any quantitative observations in support of the following statements, they seem worth including shortly in this account and represent the accumulated experience of those of us who have been employed on the work:

(a) When the bird shuffles on the perch there is a sudden large efflux of heat over a period of the order of 10 sec., comparable in amount with that evolved on rising to the standing posture. A similar efflux takes place when it flaps its wings.

(b) If the bird stretches its neck actively in any direction so that the feathers on it separate there is a fairly large increase of metabolism of the order of 20 % but very variable. If the stretching occurs in a downward direction because the bird has fallen asleep with its head on the floor of the calorimeter (a not infrequent occurrence) a small increase of metabolism is often observed, possibly representing a difference between the increase due to neck stretching and the decrease due to sleeping.

(c) Crowing produces a considerable momentary increase in heat evolution, but smaller than in the case of shuffling and standing: partly due to stretching of the neck and partly perhaps to vaso-dilatation in the comb. Persistent crowing in the early morning can increase the mean heat production considerably.

(d) When the bird goes to sleep with its head under its wing the metabolism at once drops about 12 % and remains at this level: possibly due to sounder sleep or perhaps to insulation of the comb and wattles.

(e) The behaviour during pecking is peculiar. If the bird makes large movements of its head and neck, and especially if it pecks its breast or abdomen there may be a large increase in the metabolism of the order

of 20 %; but if it pecks its back, in a position rather similar to the "head under wing" position, the rise in metabolism is much smaller. Both these types of pecking involve considerable exercise; but in the first type the neck is stretched in such a way as to cause the feathers to rise and there may be some ruffling of the feathers all over the bird. In the second type on the other hand the feathers are not greatly disturbed.

The great influence of feather insulation on heat output is also shown in the experiments of Benedict *et al.* (1932) and Gerhartz (1914). Benedict *et al.* found that the basal metabolism of the Frizzle fowl and of the moulting bird was above normal; while Gerhartz also found an increase of metabolism during moulting. The possibility of some physiological effect in moulting is of course not excluded. It appears from our experiments that the insulating power of the feathers and the effective cooling surface are more important than muscular work in causing short-period changes in metabolism in the course of a few minutes; but this is not necessarily the case over periods of considerably greater length.

Summary

An investigation of the metabolism of a number of Light Sussex cockerels has shown that there exists a rhythm in the metabolism during fasting amounting to about 9 % as between morning and night observations, the former being the higher by the percentage stated.

Two methods were adopted to exclude the effect of variation in the activity of the birds at different times of day. In the first, the birds were artificially stimulated during the normal period of repose in such manner as to give periods of approximately equal activity by day and by night. In the second, the movements of the birds were recorded by a system of "point scores", and regression equations were deduced from a large number of such experiments so as to make it possible to reduce the metabolism observations to a basis of zero activity.

The results obtained by these two methods of procedure were in good agreement with one another.

The metabolism in the *standing* position is 40-45 % above that in the sitting position, a figure considerably above that for the increase of metabolism as between the lying and standing positions usually found in quadrupeds, while at the moment of rising the heat output may occasionally be trebled, but averages about cent per cent above sitting. The former of these observations is of importance in estimating food requirements as our experiments show that generally speaking rather

more than 12 out of each 24 hr. period is spent standing when the birds are kept in cages. It follows that the sitting metabolism must be increased to allow for this when the figure is being used for computation of rations. The large heat increase on rising to the standing posture is of such short duration as to exert little influence on the mean metabolism over a 24 hr. period.

Our thanks are due to Mr G. A. Childs for his unselfish assistance throughout the work and it is a pleasure to express them here.

REFERENCES

Barott, H. G., Fritz, J. C., Pringle, E. M. & Titus, H. W. (1938). *J. Nutrit.* **15**, 145.

Benedict, F. G., Landauer, W. & Fox, E. L. (1932). *Bull. Storrs agric. Exp. Sta.* **177**.

Breirem, K. (1936). *Beretn. Forsógslab., Kbh.,* **170**.

Brody, S. (1938). *Res. Bull. Mo. agric. Exp. Sta.* no. 274.

Deighton, T. (1929). *J. agric. Sci.* **19**, 140.

Dukes, H. H. (1937). *J. Nutrit.* **14**, 341.

Gerhartz, H. (1914). *Pflug. Arch. ges. Physiol.* **156**, 1.

Mitchell, H. H., Card, L. E. & Haines, W. T. (1927). *J. agric. Res.* **34**, 945.

Mollgaard, H. (1923). *Beretn. Forsógslab., Kbh.,* **111**.

Nichita, G. & Mircea, I. (1933). *Ann. Inst. nat. Zootech. Rouman.* **2**, 45.

Report (1935). *Conference on Energy Metabolism. State College, Pennsylvania.*

Tepper, R. H. & Hellebrandt, F. A. (1938). *Amer. J. Physiol.* **122**, 563.

SOME EFFECTS OF FERTILIZER INTERACTIONS ON GROWTH AND COMPOSITION OF THE POTATO PLANT

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With G. A. COWIE

(With Twelve Text-figures)

INTRODUCTION

OBSERVATIONS that potato plants fertilized with nitrogen and phosphates may develop the conditions of the leaf usually associated with potassium deficiency, sooner, or to a more marked extent, than when fertilized with nitrogen only, have been made by one of us (Cowie, 1938).

An inspection of potato plants growing on soil poor in available phosphate but well supplied with nitrogen may fail to detect the potassium deficiency from which the plants are suffering, a condition quite different from the marked effect on the plants produced by abundant nitrogen and phosphate, but deficient potassium. In the former case, the only simple and certain way of revealing the deficiency is a replicated experiment testing the effect of potash manures on yield of tubers. These leaf symptoms of potash deficiency may be absent on plots fertilized with either nitrogen or phosphates but occur where these fertilizing elements are combined, especially when the nitrogen supply is at a high level. The symptoms may also develop under solely nitrogenous manuring if the soil is rich in available phosphate. They are, therefore, clearly due to harmful changes which occur within the plant which has access to abundant and readily available supplies of nitrogen and phosphorus, but to insufficient potassium, since the effects do not occur if supplies of all three elements are adequate.

In field experiment terminology these effects would be described as due to "fertilizer interactions".

In an attempt to obtain an insight into the manner in which the interaction of nitrogen and phosphates affect the composition of the plant and the yield of the final crop, the work described in this paper followed the general plan of comparing at several stages of growth the

composition and weights of nutrients in plants and parts of plants, grown in the field under various conditions of fertilization. The study of those plants which were grown under complete fertilization with NPK in the ratios that field experiments have demonstrated to be about optimum, can therefore be regarded as a study of the normal process of nutrient intake in the potato plant. This investigation is, therefore, mainly concerned with the comparison of plants completely fertilized and which show normal growth, with plants fertilized with nitrogen and phosphates, singly and combined.

NATURE OF SOIL, DESIGN OF FIELD TRIAL, PLANT OBSERVATIONS AND RESULTS OF FERTILIZER TREATMENT ON YIELD OF TUBERS

In order to obtain field conditions likely to give marked indications of potash deficiency, considerable care was exercised in the choice of the site, the one finally selected being a flat field on the glacial sand and gravel at Noakes Farm, Boxted, near Colchester, on which no potassic manures had been used for some years. The readily extractable P_2O_5 and K_2O contents of this soil are given and are of interest in view of the marked response obtained by the use of sulphate of potash.

mg. per 100 g.

	P_2O_5	K_2O
1% citric acid method	17	5
Acetic acid method	5	5

Reaction pH 4·9

Each mode of fertilization was replicated four times, the lay-out design being four randomized blocks of six plots each of 1/60 acre represented by the following treatments:

Nil, P, N_2, N_1P, N_2P. N_2PK,

where the treatments per acre are: P, 5 cwt. superphosphate; N_1, $1\frac{1}{2}$ cwt. sulphate of ammonia; N_2, 3 cwt. sulphate of ammonia; and K, 3 cwt. sulphate of potash.

The fertilizers were applied on 5 April 1938 and the variety "Majestic" was planted on the following day when both fertilizers and potatoes were covered by splitting the ridges. In consequence of drought (rainfall about one-quarter of the normal) the plants did not appear above ground until 3 June, when the plots were practically uniform in numbers of plants. At an early stage the appearance of some of the plots indicated that symptoms of potassium deficiency would become marked, although

at the date at which our first sample was drawn, viz. 21 June, these symptoms were not perhaps obvious to persons less well acquainted with their features. The characteristic symptoms occurred only on the N_2P and N_1P plants, appearing earlier and more markedly on the former than on the latter. The tops of N_2P plants also died down before N_1P plants, in both cases becoming black-brown in colour. The Nil and P plants were spindly with small leaves and died down soon after the N_1P plants, some showing a slight browning and others a natural yellowing of the leaves. The N_2 and N_2PK plants remained green for longer periods, the latter being the last to die down, with normal yellowing of the leaves in both cases.

On 21 June and at subsequent fortnightly intervals until the crop was finally lifted on 14 September, four entire plants from each plot were removed to the laboratory for examination. The plants were selected at random by throwing a wire ring with the eyes closed and taking the plant on which it fell. Allowing for the number of plants removed for study, the final yields of tubers from each treatment, based upon the weights from 1/88 acre and the original number of plants on each plot, were as under:

Treatment	Tubers as tons per acre
Nil	2·39
P	2·72
N_2	3·18
N_1P	2·56
N_2P	2·09
N_2PK	9·04
Mean	3·66
Standard error	0·39

It will be seen that the only significant difference between Nil and the various treatments was shown by the N_2PK plots, the difference here being highly significant.

The difference between the N_2 and N_2P plots was just significant and indicates a depression in yield by the addition of P in the presence of N_2 and in the absence of K.

The difference between the N_2P and the N_2PK plots was highly significant and indicates the very strong response to K.

TREATMENT OF PLANTS ON ARRIVAL AT LABORATORY

On the various sampling dates the entire plants lifted from each plot were placed upright in strong paper bags of large size, and these immediately placed in metal bins with well-fitting lids marked to denote

the plot series. The period from sampling to commencing work on the samples in the laboratory was approximately $1\frac{1}{2}$ hr. and wilting was reduced to a minimum. The tops were first severed at the part of the stem which best indicated the dividing line between above- and below-ground portions; the latter portion with the roots attached and after removal of tubers is in this paper termed "roots".

In the earlier samples the tops were quickly weighed in their entirety, but with increased size the leaves were cut from the stem and both weighed and analysed separately. The tops, or stems and leaves, from each plot series were separately bulked and the whole or a large portion cut up finely with scissors and secateurs, from which a large sample was dried at 100° C. for determination of dry matter. The remainder of the samples were dried on shallow trays, at about 70° C., until sufficiently dry to grind in a Christy and Norris mill. With the facilities at our disposal this drying was often accomplished overnight.

After removal of the tops, the tubers from each plot were replaced in their bags until the tops from all the plots had been dealt with as above. The tubers from each plot were washed, dried on cloths and blotting paper and weighed, then bulked according to plot series and a large sample minced by machine for dry-matter determination and for drying, grinding and preservation. In the case of the "roots" these were washed free from adhering soil, dried on blotting paper and bulked in plot series without previous weighing. They were then cut finely with scissors, weighed when air dry, ground for analysis and immediate determination of dry matter. The green weights of tops and tubers from each treatment (excepting N_2PK) at each sampling together with means and standard errors are given in Appendix, Table A.

Methods of analysis employed

The following determinations were made on each sample:

Dry matter. By drying large samples to constant weight at 100° C.

Total nitrogen. By Kjeldahl-Gunning method.

Protein nitrogen. By Barnstein's method.

Phosphorus. By wet oxidation of the organic matter followed by precipitation with ammonium molybdate and magnesia mixture.

Potassium. By precipitation with perchloric acid after removal of bases.

Calcium. By oxalate-permanganate titration.

Chlorine. By the wet oxidation method of Davies.

Table I. *Percentage of dry matter. Sampling dates*

Treatment	21 June	4 July	18 July	3 Aug.	15 Aug.	29 Aug.	12 Sept.
			Tops				
Nil	14·1	15·8	14·3	19·2	21·9	28·9	—
P	13·7	15·6	14·1	16·0	21·1	25·5	—
N_2	14·3	14·3	13·6	18·2	21·5	21·3	—
N_1P	13·4	14·4	14·7	17·9	18·9	26·6	—
N_2P	14·3	15·3	14·4	23·4	28·4	31·1	—
N_2PK	12·6	13·0	12·0	14·4	12·7	13·1	13·6
			Tubers				
Nil	16·3	20·0	18·9	21·5	21·5	21·5	—
P	16·7	20·0	18·5	23·0	21·9	23·2	—
N_2	18·7	19·1	18·5	21·2	21·5	21·6	—
N_1P	18·5	18·6	18·8	22·2	21·0	21·5	—
N_2P	19·2	20·5	18·3	20·7	19·8	20·3	—
N_2PK	18·1	19·1	18·9	21·8	21·0	22·1	22·1

Discussion of Table I

The figures for tops in this table and the subsequent graphs were obtained from separate analyses of leaves and stems and their weights, except in the case of the young plants of the two early samplings. For reasons of space the separate figures are not recorded.

As far as the tubers are concerned, an ordinary analysis of variance reveals no significant difference in dry matter content due to plot treatment, but there are obvious differences in the corresponding tops. The table is of interest for the indication it gives of the premature ripening of the plants from all other treatments when compared with N_2PK. It will be seen that the N_2P treatment induced the earliest ripening and that it sharply contrasts with N_2 treatment.

PERCENTAGE COMPOSITION OF DRY MATTER

Discussion of Graphs I–VI. Nitrogen. The very high nitrogen content of the dry matter of potato tops may be noted. According to manurial treatment, this was equal to 30–43 % of protein. The general trend of decrease in nitrogen percentage in tops and roots with increasing age, and the higher nitrogen content of these brought about by nitrogenous manuring, is apparent. The tubers of the plots incompletely fertilized tend to remain reasonably constant throughout growth and in marked contrast with those of the N_2PK treatment, in which the nitrogen content declines. Comparison of the tubers from the plots which received nitrogen, indicates the highest nitrogen content in the case of the N_2P treatment and that this is most marked in the later stages of growth. The tops and roots of these plants show the same tendency in the early
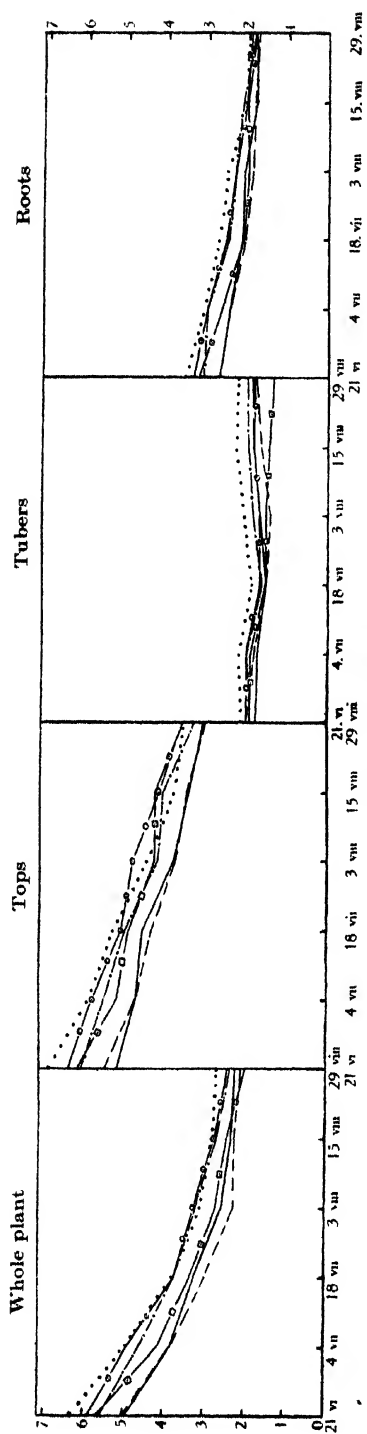
Graph I. Percentages of nitrogen in dry matter of potato plants.

Graph II. Percentages of phosphorus (P_2O_5) in dry matter of potato plants.

Nil ——— P — — — — N_2 — ⸱ — ⸱ — N_1P — — — — N_2P ⸱⸱⸱⸱⸱⸱⸱⸱⸱ N_2PK —▢—▢—
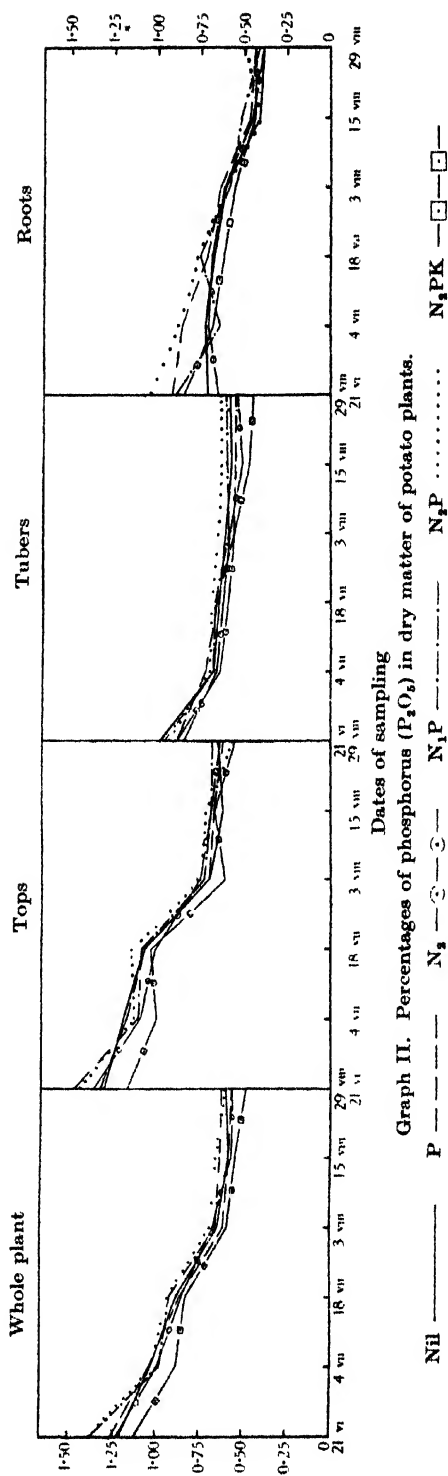
stages. With the exception of the very early stage of growth, N_2P has, however, not resulted in a higher nitrogen content of the whole plant over those fertilized with nitrogen only. The effect of the K in the N_2PK treatment was to lower the nitrogen content of tops and of roots in the early stages; tubers were affected similarly, but more markedly, later.

Proportion of nitrogen as protein. Although the results are not given, determinations of "protein nitrogen" were made throughout the investigation. The following remarks can be made regarding the percentage of the total nitrogen present as protein during growth. In the whole plant, the proportion fell steadily from 70 to 60 %; in the tops, omitting the N_2PK plants, in which there was little increase, the proportion rose from 68 to 80 %. In the tubers, omitting those from the N_2P plants, the percentage fell from 86 to 46. The tubers from the N_2P plants contained less of their nitrogen as protein at all stages, the proportion varying from 70 to 45 %. The higher proportion of non-protein nitrogen in the tubers from this treatment is in accord with the findings of Weijert & Stichr (1933), who found more amide nitrogen in the tubers from high nitrogen and low potash manuring.

The roots of the plants from the plots which received nitrogen contrasted sharply in this respect with those from which it was withheld. Between the earliest stage and maturity the proportion of the nitrogen as protein in the roots of the plants of the nitrogen series increased from 60 to 75 % and in those of the no-nitrogen series from 70 to 80 %, i.e. at all stages of growth the roots of the nitrogen-fertilized plants contained a higher proportion of non-protein nitrogen. The former roots also contained a higher percentage of non-protein nitrogen in the dry matter.

Phosphorus. The graphs indicate the general trend of the decrease in phosphorus content, in all parts of the plant, throughout growth. Although manurial treatment had evidently less effect on the concentration of this element than on the others determined, the higher content in the roots of the young plants of the P and N_2P treatments, is worthy of note. Comparison of N_2P with N_2PK indicates a significant depression in phosphorus content due to potash manuring; a depression also observed by Wallace (1929) in the case of fruit trees. The graphs also indicate that the phosphorus content was not increased by P alone but was increased by NP.

Potassium. Compared with other elements, the graphs show a much greater fall in the concentration of potassium in the tops and roots throughout life, with the exception of the N_2PK plants. At maturity,
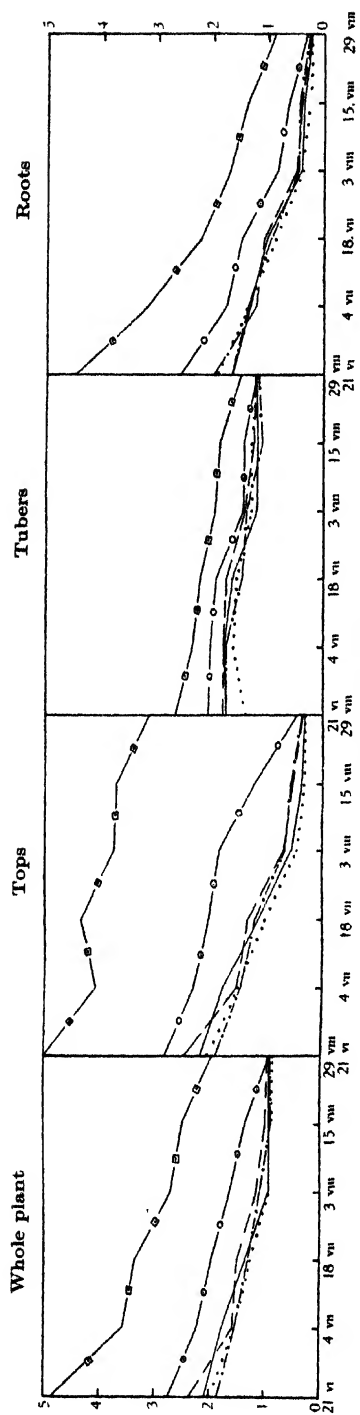
Graph III. Percéntages of potassium (K₂O) in dry matter of potato plants.
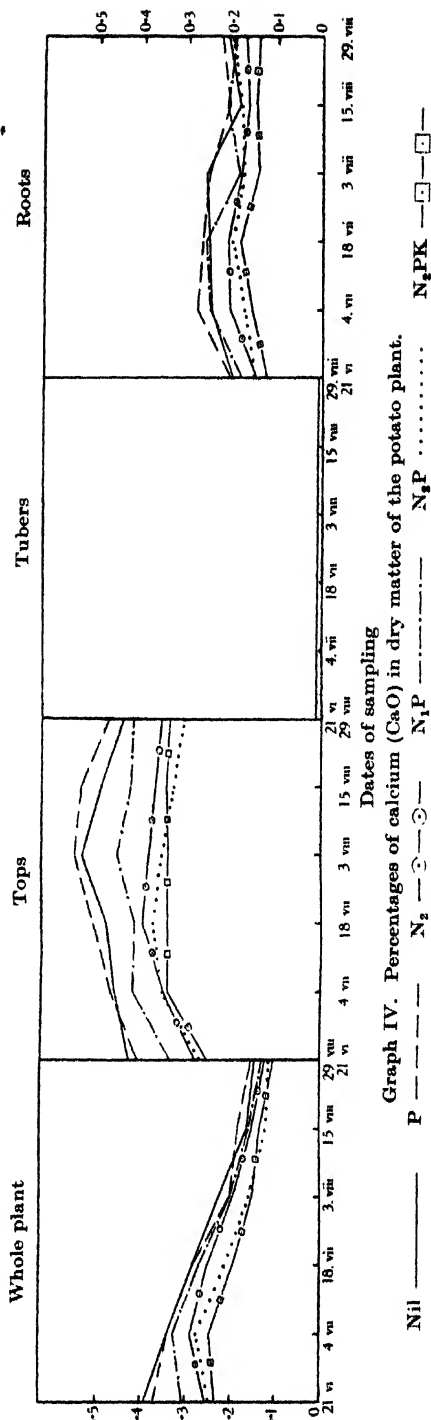
Graph IV. Percentages of calcium (CaO) in dry matter of the potato plant.

Nil ——— P — — — — N₂ — · — ⊙ — · — N₁P — · · — · · — N₂P · · · · · · · · · · N₂PK — ·□· — ·□· —
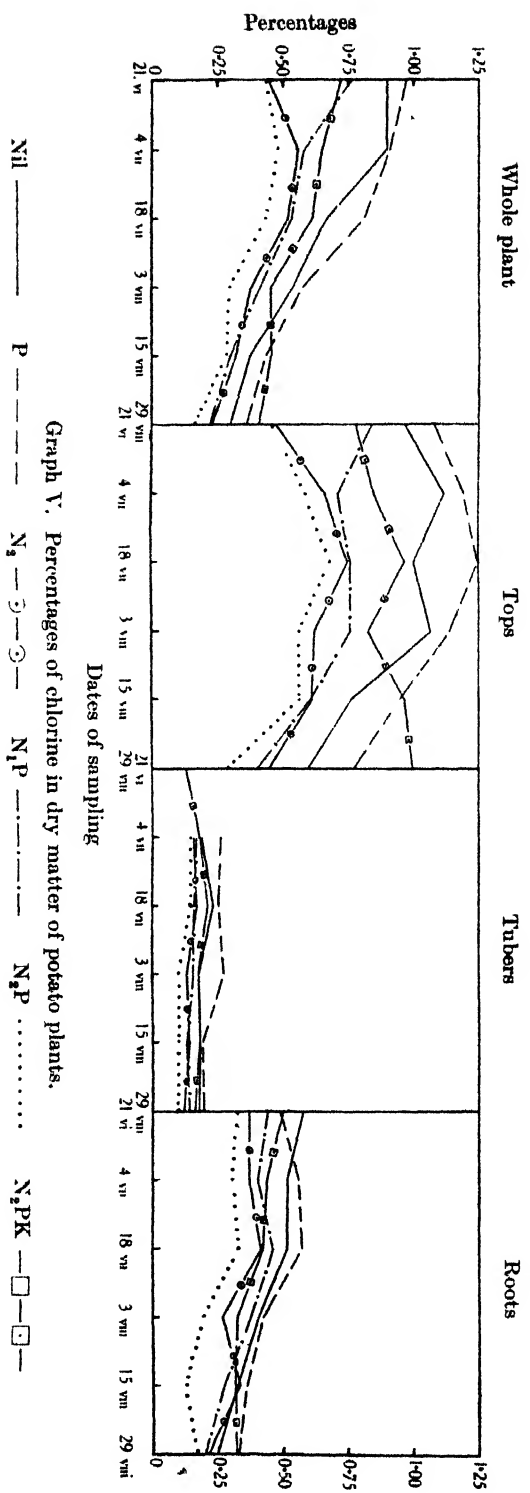
Graph V. Percentages of chlorine in dry matter of potato plants.

Percentages

Whole plant

Tops

Tubers

Roots

Dates of sampling

Nil ——   P —— ——   N₁ —⊙—⊙—   N₁P —·——·—   N₂P ········   N₂PK —▢—▢—

the concentration in these potash-deficient plants decreased to approximately one-seventh of that present at the initial stage. The much higher potassium content of all parts of the N_2PK plants gives a certain criterion from which to assess the relative potassium deficiency of the plants from the remaining treatments. Nitrogen has clearly had a beneficial effect on the absorption of potassium, but the effect is antagonized by the phosphorus in the NP treatments; the antagonism is due to interaction since P had no adverse effects. This antagonism was noted by Thomas & Mack (1938), who also worked with the potato plant. The marked increase in potassium content due to N_2 makes it appear probable that a treatment with N_1 would affect the potato plant in a similar but
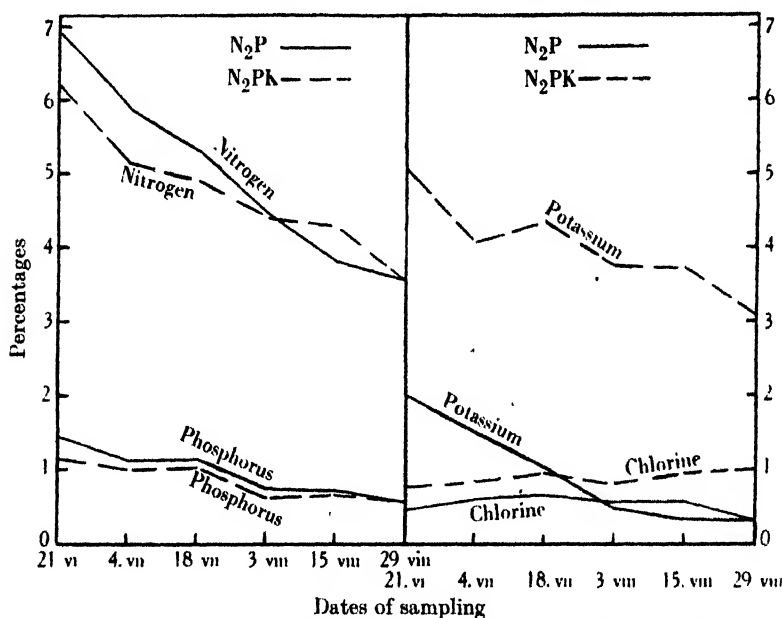
Graph VI. Percentages of nutrients in dry matter of tops of N_2P and N_2PK plants.

less marked manner. On the assumption that such would be the case and that the effect of P would be constant, N_1P plants should have a lower potassium content than N_2P plants. With the possible exception of the very early stage, there is, however, no material difference in the potassium contents of the N_1P and N_2P plants examined. From this it would appear that phosphorus is more antagonistic to potassium absorption when used in conjunction with N_2 than with N_1; an aspect considered later in a discussion of the absolute amounts of absorbed nutrients.

Calcium. The trend of the percentage of calcium in roots and tops throughout life is in very marked contrast to that of potassium. From

early stage to maturity, the figures rise and then fall slightly; the final concentration in the roots and tops being higher than in the early stages. During the same period the percentages in the whole plant fall, due to the decreasing content of calcium in the tubers and to their greatly increasing weight. As far as the plot treatments affected the composition of the parts of the plant, the concentration of calcium in the tubers is not significantly different. The well-known effect of nitrogenous manuring in depressing the calcium content of plants is well shown; for example, the average percentage in the tops was $4 \cdot 83 \%$ on the no-nitrogen plots and $3 \cdot 58 \%$ on the remaining plots, all of which received nitrogen. It is also shown by the difference in composition of N_1P and N_2P plants, the averages being $4 \cdot 12$ and $3 \cdot 50 \%$ respectively. The roots of the corresponding plants are affected similarly. The antagonism of potassium and calcium is shown by the lower figure for the latter in both tops and roots of the N_2PK plants.

Chlorine. With the exception of the tops of the N_2PK plants, the concentrations of chlorine in all parts of the plant fall from the maxima reached about 6 weeks before harvest. The main effect of plot treatment is the very marked influence of nitrogenous manuring in depressing the content of chlorine. The effect is less marked on the N_1P than on the N_2P plants. The plants from the P plots have higher chlorine contents than those from the untreated plots, but comparison of N_2 with N_2P plants indicates that phosphorus in conjunction with high nitrogen depresses chlorine content. Potash manuring in the presence of adequate nitrogen and phosphate increased chlorine concentration.

RATIOS OF NUTRIENTS DURING GROWTH ·

Ratios of some nutrients at each sampling date for the whole plant and parts of the plant have been calculated, and are shown in the case of the tops in Table II. The effect of manurial treatment on the ratios of the elements in the plants is best seen in the tops and roots, the variations in the tubers being far less pronounced. Generally speaking, the variations during growth were much less marked in the plants of the N_2PK treatment than in the plants with unbalanced manuring, the effect of the potash manuring being to narrow the ratios of other elements in relation to potassium. To a less marked extent the ratios in the N_2 plants were affected in a similar manner to the N_2PK plants, except during the last fortnight, when, as noted later, a loss of potassium occurred.

Considering the N/K_2O ratios, to which great importance is attached in the case of fruit-tree leaves, it is interesting to note the narrow and

Effects of Fertilizer Interactions

approximately constant ratios in the tops of the N_2PK plants, which contrast, very markedly, with the much wider ratios, particularly in the later stages, in the tops of plants of other treatments. Thus the N/K_2O ratios of the tops of the N_2PK plants vary from 1 to 1·2 only, while those of the N_2P plants which show the widest ratios vary from 3·4 to 12. It is obvious that with the N_2PK plants, the nitrogen and potassium migrate to the tuber in about the same proportion as received by the tops throughout the period covered by the investigation. With all other

Table II. *Ratios of nutrients in tops during growth*

	21 June	4 July	18 July	3 Aug.	15 Aug.	29 Aug.
			N/K_2O			
Nil	2·39	2·65	3·95	6·91	9·30	10·26
P	2·23	3·08	3·27	5·41	6·48	6·85
N_2	2·29	2·49	2·50	2·68	3·38	7·77
N_1P	3·23	3·74	4·15	6·26	7·47	10·97
N_2P	3·38	3·93	4·30	9·47	11·99	11·79
N_2PK	1·23	1·27	0·98	1·14	1·15	1·14
			N/P_2O_5			
Nil	3·98	3·97	4·26	4·35	5·56	4·68
P	4·14	4·02	4·06	5 37	5·27	4·86
N_2	4·68	5·28	5·07	6·56	6·14	5·65
N_1P	4·15	5·00	4·60	5·73	5·94	4·81
N_2P	4·77	5·22	3·89	5·93	5·32	6·33
N_2PK	5·30	5·19	4·08	7·03	6·24	6·09
			CaO/K_2O			
Nil	1·98	2·59	4·19	9·69	13·33	14·91
P	1·67	3·06	3·86	7·95	9·99	13·50
N_2	1·01	1·53	1·95	2·08	3·01	7·68
N_1P	1·78	2·87	3·49	6·83	7·80	13·65
N_2P	1·35	2·37	3·63	7·57	10·50	10·20
N_2PK	0·50	0·84	0·79	0·91	0·97	1·08
			Cl/K_2O			
Nil	0·45	0·66	0·86	1·93	2·04	1·93
P	0·44	0·77	0·99	1·64	1·76	2·21
N_2	0·17	0·29	0·37	0·34	0·50	0·98
N_1P	0·45	0·48	0·63	1·13	1·11	1·35
N_2P	0·23	0·39	0·66	1·20	1·78	0·94
N_2PK	0·15	0·21	0·22	0·22	0·26	0·32
			P_2O_5/K_2O			
Nil	0·60	0·67	0·93	1·26	1·67	2·21
P	0·54	0·76	0·80	1·01	1·23	1·77
N_2	0·49	0·47	0·49	0·41	0·55	1·38
N_1P	0·78	0·75	0·90	1·09	1·25	2·28
N_2P	0·71	0·75	1·10	1·59	2·25	1·86
N_2PK	0·23	0·24	0·24	0·16	0·18	0·19
			N/CaO			
Nil	1·20	1·02	0·94	0·71	0·70	0·69
P	1·34	1·01	0·85	0·68	0·65	0·64
N_2	2·27	1·63	1·28	1·29	1·12	1·01
N_1P	1·81	1·30	1·19	0·92	0·96	0·80
N_2P	2·51	1·66	1·19	1·25	1·14	1·15
N_2PK	2·46	1·51	1·24	1·25	1·19	1·06

treatments the migration of potassium was relatively more rapid than that of nitrogen. In the roots of the N_2PK plants, the ratios N/K_2O vary throughout growth from 0·7 to 2·0, while in the roots of the N_2P plants the corresponding figures are 1·9 and 9 respectively.

Another ratio which shows marked variations during the growing period is CaO/K_2O, the figures varying from 0·5 in June to 1·1 in late August in the tops of the N_2PK plants, while the tops of the N_2P plants show variations during the same period from 1·3 to 10·2. On the other hand, little variation is seen in the ratios N/P_2O_5 during the growing period, or between the plants receiving different manurial treatments.

FORTNIGHTLY VARIATION IN WEIGHTS OF NUTRIENTS IN SIXTEEN PLANTS FROM EACH FERTILIZER TREATMENT

These weights are presented in the case of whole plant, tops and tubers in Graphs VII·XI, the roots being omitted for reasons of space, although discussed in the text.

Nitrogen. It is evident that no significant loss of nitrogen from any of the plants was observed. The plants on the N_2P treatment attained maximum quantity by 18 July, those on the Nil, P and N_1P, by 3 August, those on N only by 15 August, while N_2PK plants were still absorbing at mid-September. The more gradual attainment of maximum quantity of nitrogen by the normally fertilized potato plant (N_2PK plots) is in marked contrast with our previous observations on wheat (Knowles & Watkin, 1931) and sugar beet (Knowles *et al.* 1934). The effect of phosphates in inducing earlier maturity is shown in the rate of uptake of all the nutrients, but is most strikingly seen in N_2P treatment, by comparison of these plants with those from N_2 plots, the former plants attaining maximum intake of nitrogen a month earlier than the latter. It is of interest to note that the N_2P plants which received 3 cwt. per acre of sulphate of ammonia, finally acquired no more nitrogen than the untreated plants, although they absorbed more rapidly. From comparison of treatments N_2 and N_2P, it is clear that the P caused a depression of nitrogen absorption to the extent of about 33 %. On the other hand, comparison of N_2P with N_2PK shows that the addition of K caused an increase of nitrogen absorption by about 250 %.

The tops of all the plants, except those of the N_2PK treatment, attained their maximum of nitrogen by 18 July, their rate of outgo being equalled by rate of income for a fortnight before the decrease set in, except in the case of N_2P. In the latter case, this period of constancy
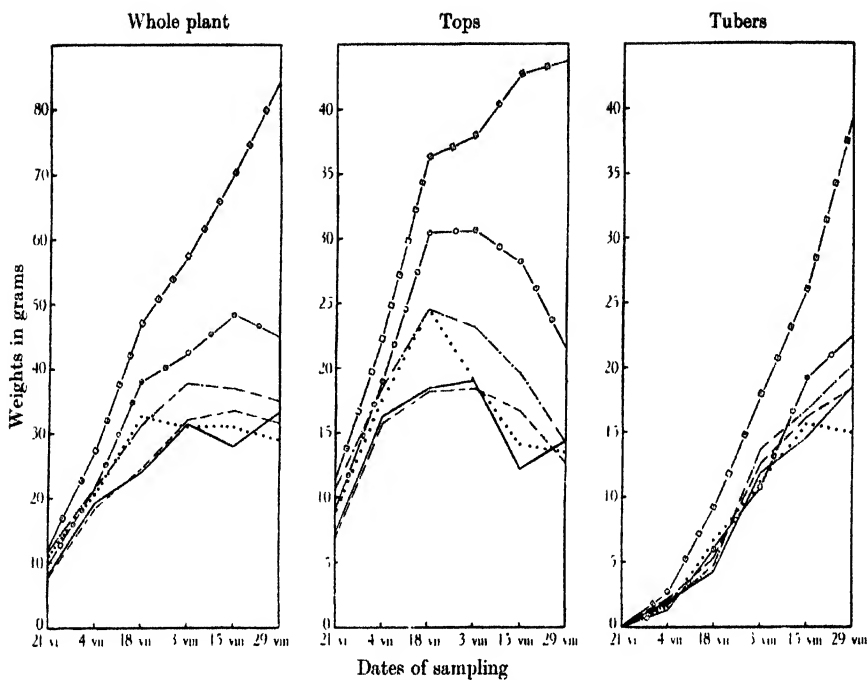
Graph VII. Weights of nitrogen (N) in 16 potato plants.
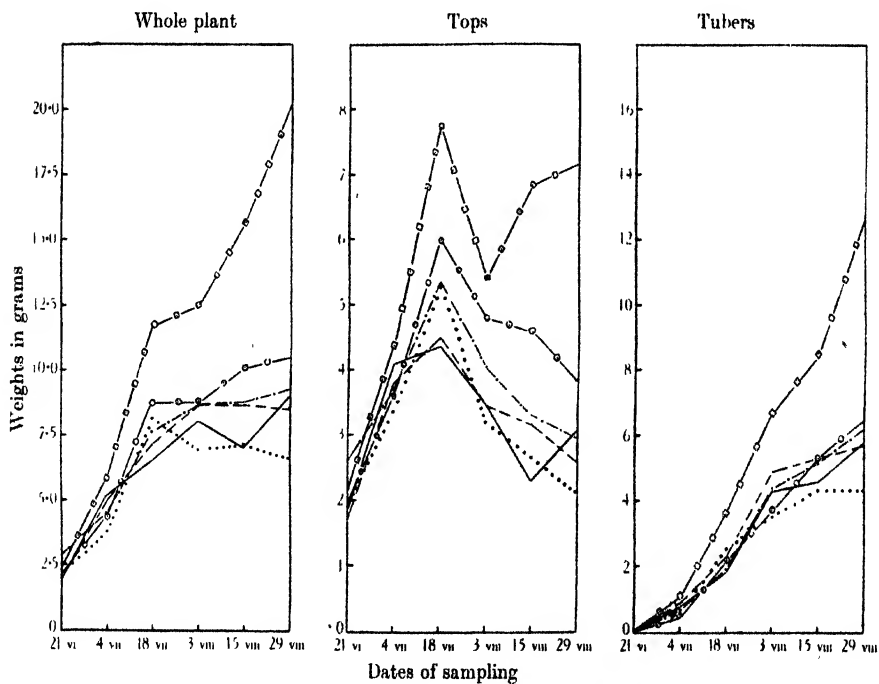
Graph VIII. Weights of phosphorus (P_2O_5) in 16 potato plants.

| Nil ———— | N_2 —·)—·(·— | N_2P ·········· |
| P — — — — | N_1P ·—·—·—· | N_2PK —▢—▢— |
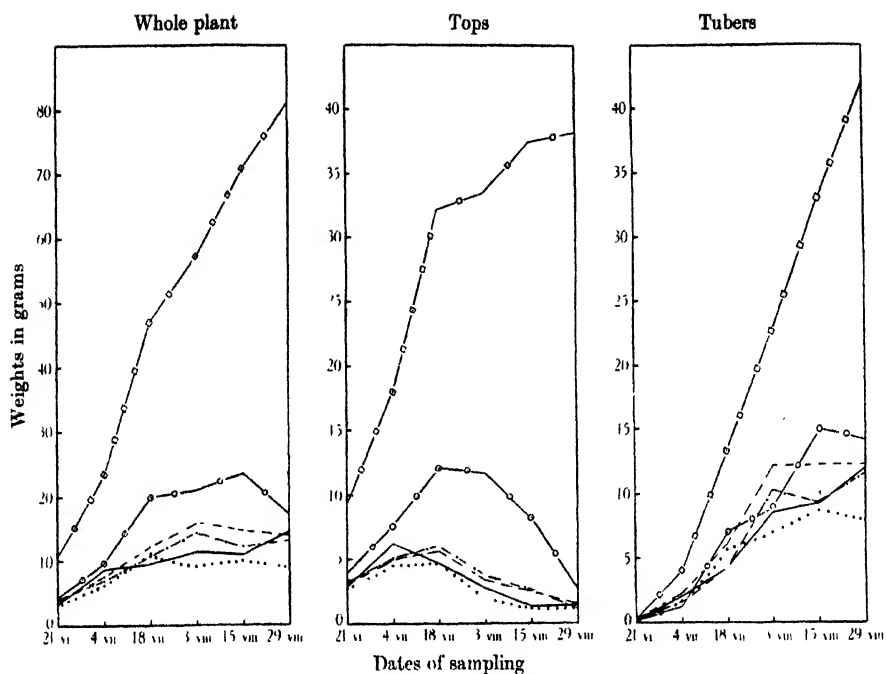
Graph IX. Weights of potassium (K_2O) in 16 potato plants.
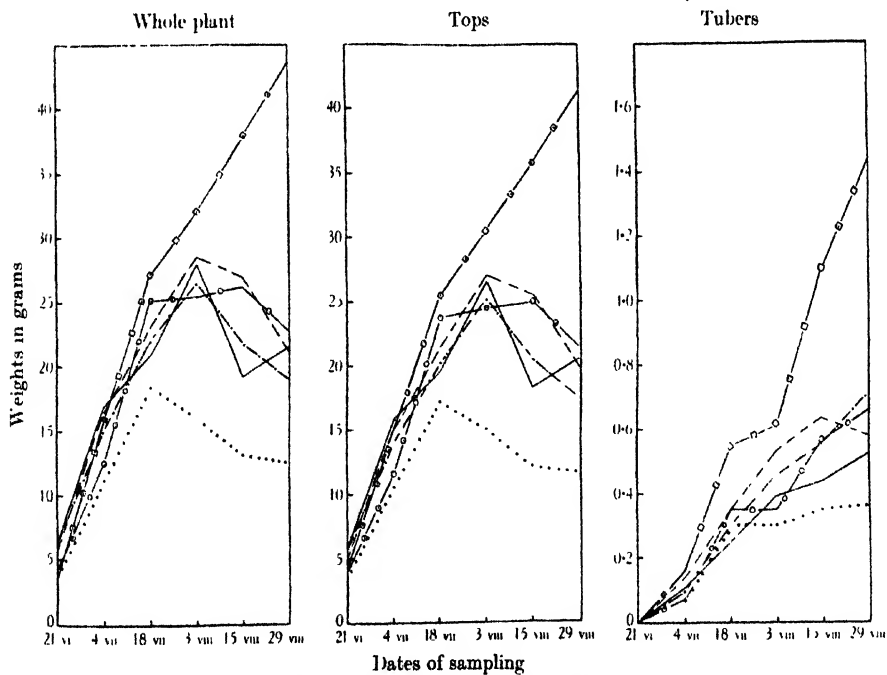
Graph X. Weights of calcium (CaO) in 16 potato plants.

Nil ——— N_2 —⊙—⊙— N_3P ··········
P — — — — N_1P —·—·—·— N_2PK —▢—▢—

in the tops did not occur, the attainment of maximum being followed during the ensuing fortnight by a sharp decline. The effect of phosphate on the N_1P and N_2P plants resulted in the attainment of maximum protein nitrogen a fortnight earlier than in the case of the N_2 plants.

In the roots, excepting those of N_2PK treatment, the maximum quantity of nitrogen was reached by the middle of July and was followed
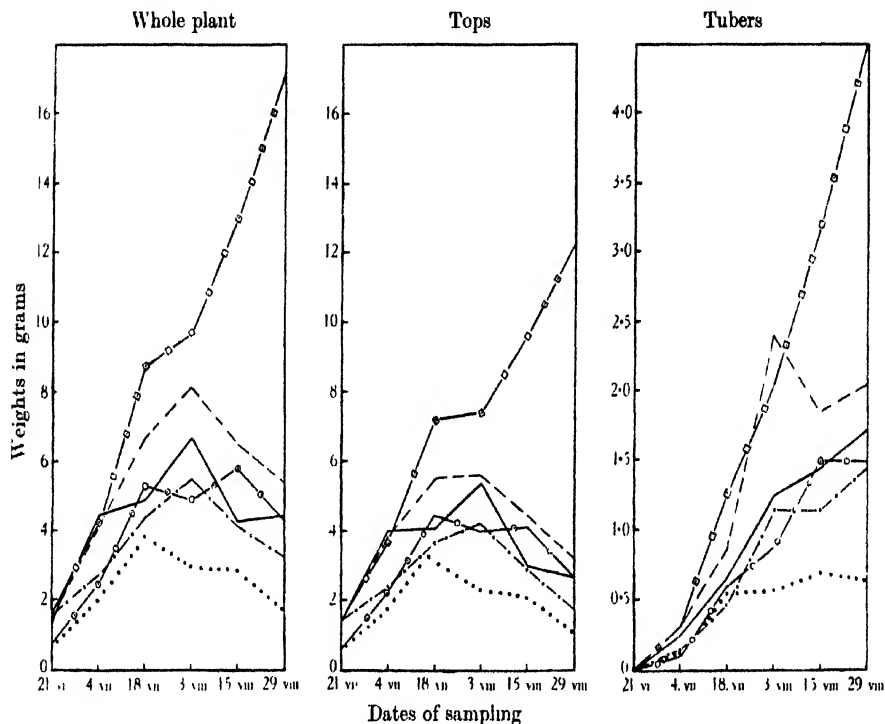
Graph XI. Weights of chlorine in 16 potato plants.

Nil —————— N_2 ——)—)—— N_2P ··· ······
P —— —— —— N_1P ····—·—·—· N_2PK ···☐—☐—

by steady depletion. The roots of the N_2PK plants, however, reached maximum about a fortnight later and showed no significant decrease up to mid-September. In contrast to all other treatments, the tubers of N_2P plants showed no gain during the final fortnight.

Phosphorus. The decrease from the maximum in phosphorus which is noted with the N_2P plants but not with others, approaches statistical significance. Phosphate-treated plants attained their maximum uptake earlier than the others, although this is not noted in the tops. The tops of the N_2PK plants, however, maintained their maximum quantity until September, whereas the others began to suffer loss by mid-July.

In contrast to all other treatments, the tubers of N_2P plants showed no increase during the final fortnight. From the point of view of a manuring experiment, it is evident that of the 5 cwt. of superphosphate applied per acre, none was recovered in the plant, unless accompanied by potash manuring.

Potassium. The plants of the N_2 treatment suffered a significant and noteworthy loss of potassium during the fortnight prior to harvest, while the loss shown by N_2P plants is barely significant. As losses of other elements will be noted a discussion of this aspect is deferred.

Phosphate manuring without potash induced earlier attainment of maximum potassium, particularly by the N_2P plants, in which it occurred by mid-July; at which time the N_2PK plants had absorbed only 40 % of their final quantity. The data support the view expressed earlier, that in manuring with phosphorus in conjunction with nitrogen, the former is antagonistic to potassium absorption, and especially so when the level of nitrogen is high. Thus in comparison with N_2 plants, those of N_2P treatment were able to absorb only about one-half of the amount of potassium. Comparison of the higher amount of potassium in the N_1P over the N_2P plants, also shows the greater antagonism of phosphorus when nitrogen is more abundant. The absorption of potassium by N_2P plants was in fact less than that of plants grown without fertilizer, and was approximately one-tenth of that of N_2PK plants.

In the later stages, the tops of the N_2PK plants contained about thirty times more potassium than those of the untreated or of the phosphated plots, and continued to gain to a much later date. The decrease in amount of potassium which occurs during the last 6 weeks in the tops of the plants without potassium manuring, is not marked in the N_2 plants. until the final fortnight.

The roots of the N_2PK plants not only contained more potassium than those of the other treatments, but also did not undergo such severe depletion during the last fortnight of the plants' growth. Little increase of potassium in the tubers of phosphated plants was noted during the last month.

It is highly significant that the period of obvious change in the appearance of the tops coincided with the period in which large decreases in amounts of potassium in the tops were noted in the case of the various treatments. For example, the tops of the N_2P-treated plants, which were the first to show symptoms of scorch, and in which the loss was greatest, lost about 60 % of their potassium during the last fortnight of July.

Calcium. With the exception of those with N_2PK treatment, losses of calcium were noted from all plants, the losses being lowest on N_2 and highest on N_2P treatments. N_2 and N_2P plants reached maximum calcium a fortnight earlier than the others, but the loss did not occur with N_2 until the last fortnight, whereas with N_2P it was spread over 6 weeks. The observations on the tops of all plants were similar to those of the corresponding whole plants. The roots of all plants attained maximum calcium by mid-July, but those of N_2P treatment were subsequently depleted more rapidly. The tubers of P and N_2P treatments reached their maxima earlier than those of other treatments.

Chlorine. Losses of chlorine occurred from the plants of all treatments with the exception of N_2PK, the N_2P plants losing more than half of the amount absorbed. N_2 plants did not suffer this loss until a month later than N_2P plants. These observations are also true of the corresponding tops. The roots of all plants attained maximum chlorine by mid-July, the depletion which followed being most rapid in the N_2P plants. The tubers of P plants were the first to attain maximum chlorine, and the antagonism of nitrogen and chlorine alluded to earlier is well illustrated by the much greater amount of chlorine in N_1P than in N_2P tubers.

LOSSES OF ELEMENTS OBSERVED

The extent of the losses from the maxima previously noted in the final plant are given in Table III.

Table III. *Percentage losses of elements*

Treatment	K	Ca	Cl	P
Nil	0	24	34	0
P	13	27	33	0
N_2	27	14	26	0
N_1P	13	29	40	0
N_2P	17	33	54	20
N_2PK	0	0	0	0

From a statistical standpoint the loss of potassium by the N_2 plants is significant, as is also the case with the losses of calcium and chlorine on all treatments with the exception of N_2PK. The loss of phosphorus from the N_2P plants which did not occur with other treatments, and the entire absence of loss of elements from the N_2PK plants, are outstanding features of the table. In previous work on wheat (Knowles & Watkin, 1931) and sugar beet (Knowles *et al.* 1934) we have noted losses; in the former plant of potassium, calcium and chlorine, and in the latter of phosphorus and chlorine. Although in the case of wheat our work was

concerned only with the aerial parts of the plant, we recorded the opinion that the losses were so large that they were not due to mechanical causes, but to a return of elements to the roots; the losses from beet were suggestive of excretion from roots to the soil.

If the assumption is made in the case of the potatoes that the roots may not have been completely removed from the soil in all cases, this could not possibly account for the losses observed, since the latter were

1, nil; 2, P; 3, N_2; 4, N_1P; 5, N_2P; 6, N_2PK

Tops ▓   Tubers ▓   Roots ☐
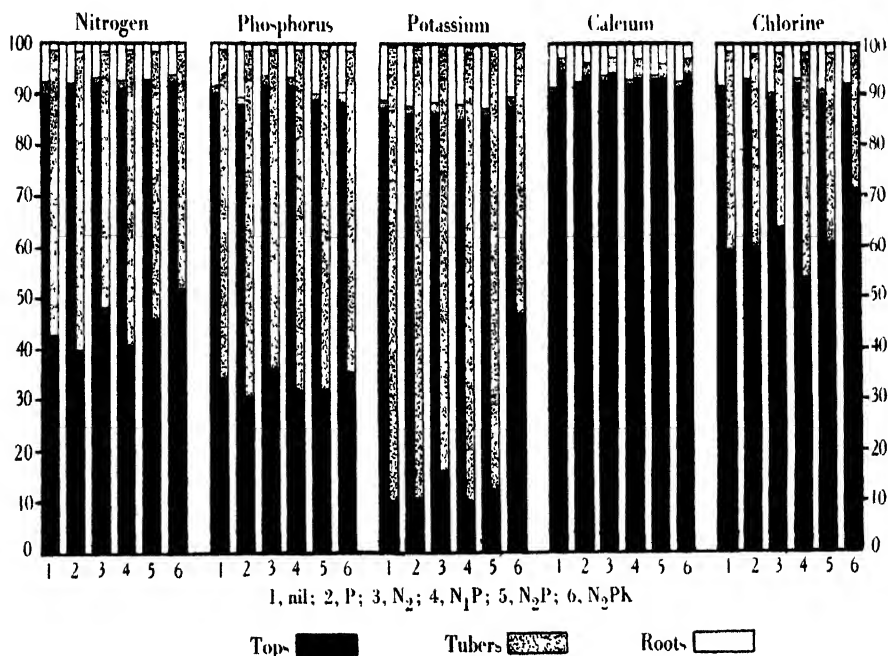
Diagram 1. Percentage distribution of nutrients in young and mature plants.

many times as great as the total weights of the respective elements in the roots. It appears reasonable to conclude, therefore, that some elements, particularly chlorine and calcium, were actually excreted from the roots to the soil. Work by Richardson et al. (1933) with *Phalaris tuberosa*, indicated that the loss of potash undergone by this plant was by actual excretion to the soil.

In view of work by Sekera (1928), it is of interest that the major losses occur with the plants which would normally be considered to have had unbalanced manuring.

Distribution of nutrients in young and mature plants

The percentage distribution of elements in parts of the plants are given in Diagram I, the intermediate growth stages being omitted to economize space. The distributions are perhaps of greater interest as a contribution to growth studies of the potato, rather than in tracing effects due to fertilization treatments. With the exceptions to be noted, the unbalanced fertilizations did not materially affect distribution of elements within the plants. In all cases calcium behaves differently from the other elements by remaining in the tops in very constant proportion, viz. on the average 92–94 % in the young and mature plants respectively. At all stages of growth the proportion of potassium in the tuber was least in the N_2PK plants; the tubers of N_2 plants also contained a smaller proportion of potassium until the last month, when they more nearly resembled those of other unbalanced treatments. These differences in distribution due to manurial treatment also occur to a smaller extent with nitrogen and chlorine.

Summary and conclusions

1. An account has been given of the percentages of nutrients in the dry matter and weights of nutrients in tops, tubers and roots of potato plants throughout growth under six fertilizer treatments.

2. Manurial treatment affected dry-matter content of tops but not of tubers.

3. Balanced manuring, as represented by N_2PK treatment, resulted in tubers in which nitrogen content of dry matter declined with age. The effect of the K was to lower the nitrogen, phosphorus and calcium contents, to increase chlorine content of all parts of the plant, and to maintain a much higher and more constant concentration of potassium in tops and roots. With unbalanced manuring the nitrogen content of the tubers was more constant.

4. Manuring with nitrogen only raised the content of potassium in the dry matter of all parts of the plant.

5. Nitrogenous manuring, whether alone or in combination, raised the nitrogen content of the dry matter of all parts of the plant, a smaller proportion of which was present as protein. Calcium and chlorine contents were lowered.

6. Phosphate manuring in conjunction with nitrogen depressed the concentration of potash in the dry matter of all parts of the plant.

7. N_2P plants were the first to attain their maximum uptake of all nutrients, namely, about 7 weeks from appearance above ground, at which time N_2PK plants had absorbed only 40% of the quantities finally noted.

8. No losses of elements were observed in the plants which received balanced manuring (N_2PK), but losses of calcium and chlorine occurred in all other plants, amounting on the average to 25 and 37 % respectively, but being highest in N_2P plants. A significant loss of potassium occurred in N_2 plants and a highly suggestive loss of phosphorus occurred in N_2P plants.

9. Manurial treatment had little effect upon the proportionate distribution of nutrients in parts of the plants with the exception of those of N_2PK treatment, in which a lower proportion of potassium was transferred to the tubers. With all treatments a high and constant proportion of calcium remained in the tops.

10. The symptoms of scorch and premature dying off of tops of potatoes which occur on soils deficient in potash, when manured with nitrogen in conjunction with phosphates, are shown to be due to decreased absorption of potassium, which the interaction of these two elements induces. By increasing the soil nitrogen the adverse effects of the combination become more pronounced. Cowie's diagnosis from leaf appearances, that these effects are due to potassium deficiency, is, therefore, well founded, and his further observation that plants fertilized with nitrogen only suffer much less, is shown to be due to the increased absorption of potassium which such treatment induces. The mechanism of the interaction is at present incapable of precise explanation, but the relatively higher concentrations of nitrogen and of phosphorus in the dry matter of the roots of the young plants manured with phosphates and with nitrogen at a high level, suggests some poisoning of the plant, which inhibits the absorption of potassium to a suitable concentration for maintaining health. This would consequently adversely affect the absorption of sufficient amounts of nutrients necessary for growth.

A copy of the primary data has been deposited in the Library of the Rothamsted Experimental Station.

REFERENCES

Cowie, G. A. (1938). *Emp. J. exp. Agric.* **6**, 315.

Knowles & Watkin (1931). *J. agric. Sci.* **21**, 612.

Knowles, Watkin & Hendry (1934). *J. agric. Sci.* **24**, 368.

Richardson, Trumble & Shapter (1933). *Bull. Commonwealth of Australia Report,* no. 66.

Sekera, F. (1928). *Z. PflErnähr. Düng.* **76**, 533.

Thomas & Mack (1938). *J. agric. Res.* **57**, 397.

Wallace, T. (1929). *J. Pomol.* **8**, 23.

Weighert, J. & Stier, G. (1933). *Prakt. Bl. Pflanzenb.* **10**, 277.

APPENDIX

Table A. *Green weights of sixteen potato plants with means and standard errors*

	Nil	P	N_2	N_1P	N_2P	Mean	S.E.
			Tops (g.)				
21 June	993	920	969	1305	925	1022	132
4 July	2178	2063	2306	2318	1955	2164	258
18 July	2856	2993	4378	3341	3782	3470	325
3 Aug.	2612	3066	3334	2968	1815	2759	340
15 Aug.	1693	2319	3156	2551	1314	2207	606
29 Aug.	1605	1648	2850	1642	1220	1793	658
			Tubers (g.)				
4 July	604	613	362	504	393	495	140
18 July	1521	1906	1953	1535	1995	1782	212
3 Aug.	3297	3830	3017	3330	2642	3223	290
15 Aug.	3716	4447	4882	4068	3566	4136	454
29 Aug.	4594	4477	5646	4709	3422	4370	691

Table B. *Grams of dry matter in sixteen potato plants at sampling dates*

Treatment	21 June	4 July	18 July	3 Aug.	15 Aug.	29 Aug.	12 Sept.
			Whole plant				
Nil	166	498	734	1248	1200	1480	- -
P	154	483	823	1412	1487	1494	—-
N_2	166	437	1018	1314	1766	1857	---
N_1P	209	465	823	1328	1370	1476	-—
N_2P	156	410	872	1000	1089	1082	—
N_2PK	215	656	1415	2125	2862	4160	5681
			Tops				
Nil	140	304	407	501	371	464	—
P	128	322	422	491	478	421	—
N_2	140	330	595	635	677	605	—
N_1P	174	335	492	555	481	436	-—
N_2P	132	299	462	425	372	379	-
N_2PK	183	438	740	891	997	1223	1473
			Tubers				
Nil	2·9	116	287	709	799	987	—
P	3·0	122	353	882	972	1040	·--
N_2	4·9	69	361	638	1050	1218	—
N_1P	6·7	94	288	738	855	1011	—
N_2P	2·8	81	365	546	690	680	—
N_2PK	8·0	166	609	1161	1793	2859	4125
			Roots				
Nil	23·4	38·1	40·1	37·8	30·8	28·4	—
P	22·9	37·9	48·6	40·1	36·9	33·2	—
N_2	20·7	37·6	61·7	40·5	38·6	33·9	—
N_1P	28·4	36·6	42·7	35·6	33·7	28·9	—
N_2P	20·9	30·1	44·3	28·8	26·5	22·9	—
N_2PK	24·3	52·3	66·0	73·2	72·1	77·6	83·5

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STUDIES WITH LUCERNE (*MEDICAGO SATIVA*)— ROW DISTANCES AND "SMOTHER" CROPS

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At the present time much interest is being taken in the preservation of greenstuff for feeding during the winter either by drying or by the use of modern methods of silage making and cheap silos. In the wetter districts of the country grass will probably be the material generally conserved, but in drier districts, and particularly on the lighter soils in such districts, grass is an uncertain crop. There appears, therefore, to be a very good case for wide extension of the cultivation of lucerne in dry districts, and already factories have been established for drying large areas of lucerne. Further, ensiling is suitable for the small farm, and consequently lucerne might find a very important place in this country.

Although lucerne has been grown in Britain since the middle of the seventeenth century, and possesses valuable drought-resisting powers, the acreage devoted to the crop is small and shows no signs of increasing. One factor which has tended to restrict the development of the crop is the short duration of most lucerne leys, which have to be ploughed up after four or five years because they then carry many weeds and little lucerne. There are two possible primary causes for the deterioration of leys. It may be that a large number of lucerne plants are killed by crown wart (*Urophlyctis alfalfae*), and that the space thus left vacant is then occupied by weeds, or it may be that weeds establish themselves and smother out the lucerne plants. In either event the end result is a foul field with few lucerne plants surviving, so that it is impossible to say what the primary cause was; in popular literature it is generally assumed that the invasion of weeds is the chief cause for deterioration.

There are several different principles which may be adopted to control weeds in a lucerne ley. General husbandry methods should ensure that the crop is sown on clean land, but even then weeds rapidly prove troublesome. Bates (1935) studied the various species of weeds in lucerne leys in East Anglia, and showed that the weed flora changes as the age of the ley increases. He suggested that a promising line of enquiry would be to sow grasses and clovers with the lucerne, in order to occupy ground space to the exclusion of weeds. Such supplementary plants are usually referred to as "smother" crops. Various writers have suggested the

inclusion of such plants as rye grass, cocksfoot, timothy, wild white clover and trefoil, but their statements have not usually been supported by direct experimental evidence. Parker (1931) described experiments in which 2 lb. of wild white clover per acre were sown with lucerne seed, and a good ground cover was obtained after the second year: his general conclusion was that this cover was only gained at the expense of the yield of lucerne, and was not worth while unless the aftermath grazing was considered valuable. In South Australia, Spafford (1931) recommended the annual drilling of cereals in a lucerne ley, with the object of increasing the total yield of green stuff, although this practice tended to kill out the lucerne.

It is frequently suggested that weeds in a lucerne ley should be controlled by cultivations. Drastic harrowing or cultivating during the winter undoubtedly gives some control, but necessarily results in some damage to the crowns of the lucerne, and the effect on yield of the ley has not been studied accurately. Drilling the crop in wide rows with the object of allowing intercultivation is another frequent suggestion, but it apparently still lacks precise experimental justification, and in practice the necessary horse-hoeing is seldom performed. Many farmers prefer to drill their rows as close as possible, or even to broadcast the seed, with the object of covering the ground. McKay (1928) in New Zealand compared the yields obtained from 7, 14 and 21 in. rows and found that the nearest rows gave the highest yield.

An experiment was laid down on the University Farm at Cambridge in 1933, the treatments being a combination of row distances and smother crops, and all yields were recorded for four harvest years. This paper describes the results from only this one experiment, but the conclusions reached have been supported by four demonstrations conducted on the same farm in recent years.

DESCRIPTION OF THE EXPERIMENT

The experiment was situated on good gravel loam in high condition, and included ninety-six plots in all. There were six blocks, of four main plots each, for the comparison of the row distances, $3\frac{1}{2}$, 7, $10\frac{1}{2}$ and 14 in. The main plots were 40 yd. long and one drill width (8 ft.) wide, and had their long sides contiguous. The drill used had coulters $3\frac{1}{2}$ in. apart. and the varying row distances were obtained by inserting cardboard sheets to direct the seed from one or more series of cups into a coulter tube; this ensured that the same seed rate (22 lb. per acre) was used on all plots. The variety used was Hungarian, and the seed was inoculated.

Each main plot was divided into four subplots (each 10 yd. long) over which three smother crops and a control were randomized; the smother crops were commercial cocksfoot (*Dactylis glomerata*) at 10 lb. per acre, trefoil (*Medicago lupulina*) at 5 lb. per acre, and wild white clover (*Trifolium repens*) at 2 lb. per acre. The lucerne was drilled first, the smother crops were then broadcast and the field rolled. This sowing was done on 12 May 1933, on bare ground.

Table 1. *Establishment and persistence of lucerne plants*[1]

	Widths of drilling					
	$3\frac{1}{2}$ in.	7 in.	$10\frac{1}{2}$ in.	14 in.	S.E. of a mean	Significance
Relative germination 8. vi. 33	116·4	112·5	100·1	100·0	4·69	Reg.*
Relative no. of stems 4. iv. 34	147·9	129·8	109·2	100·0	7·08	Reg.***
Relative no. of stems 9. iv. 35	149·1	136·7	112·7	100·0	4·53	Reg.***
Relative no. of stems 17. iv. 36	184·5	189·1	129·6	100·0	6·95	Reg.** Devs.**

	Smother crops					
	Cocksfoot (C)	Wild white clover (W)	Trefoil (T)	Nothing (O)	S.E. of a mean	Significance
Relative germination 8. vi. 33	95·8	101·4	103·3	100·0	3·01	Insig.
Relative no. of stems 4. iv. 34	71·9	93·9	86·6	100·0	2·30	O>C, T** W, T>C** W>T*
Relative no. of stems 9. iv. 35	68·6	100·5	100·3	100·0	2·50	W, T, O>C***
Relative no. of stems 17. iv. 36	95·3	101·0	97·8	100·0	3·66	Insig.

[1] *Note.* In this and subsequent tables:

* Denotes significance $P<0.05$.
** ,, ,, $P<0.01$.
*** ,, ,, $P<0.001$.

A germination count was made on 8 June 1933, when it was found that the competition between the thicker plants within the wider rows reduced establishment to some extent. The differences which are given in Table 1 were just significant. Over the whole experiment establishment could be described as good. Growth was rather slow owing to the dry weather in the latter half of the summer, and only a light growth was available for cutting in August; at this cut no experimental weighings were made. Establishment was not affected by the smother crops. In the springs of 1934, 1935 and 1936, counts of the number of stems were made on sample quadrats, the total area of these on each plot being one-fortieth of the plot. Table I shows that narrow spacings carried many more stems than the wide ones, the differences being highly

significant in all cases. Cocksfoot proved aggressive throughout, the reduction in stem number in the first two years being significant. In the first year trefoil also reduced the number of stems but it had no effect subsequently as it died out completely by the end of 1934. All smother crops established themselves rapidly, and with cocksfoot and trefoil establishment did not appear to be affected by the distance between the lucerne rows. Wild white clover, on the other hand, gave a considerably better cover on the plots with wide lucerne rows, this difference persisting throughout the experiment. During 1936 it was seen that many lucerne plants were affected with crown wart and during the subsequent winter many plants died out. In April 1937, the plant was so thin that no stem count was made, but the experiment was persisted with until after the June cut when the area was ploughed up.

YIELDS FROM EXPERIMENTAL CUTS

Two experimental cuts were made in 1934, three in 1935 and in 1936 and a final one in 1937. The method employed was to cut by hand discards 2 ft. wide across the ends of all subplots, and then to cut the plots themselves with an ordinary grass mower. This method allowed a cut space of 4 ft. between two subplots, which proved amply sufficient for the cutter bar of the mowing machine to clear itself. The two swathes for each subplot were raked up and the material weighed; samples were then taken from each subplot for the determination of dry matter. The results obtained are shown in Table II where the first, second and third cuts of each season have been grouped together.

Width of drilling had little effect on the first cuts of each season; the general tendency was for the narrower rows to yield more highly than the wider rows, but this was only significant in 1935 and was insignificant for the total of four years. At the July and August cuts, however, the narrow rows were considerably better than the wider ones, the regression being significant in all except one case. Over the whole period, the $3\frac{1}{2}$ and 7 in. rows yielded approximately half a ton of dry matter per acre more than the $10\frac{1}{2}$ and 14 in. rows. In February 1937 estimations of the proportion of ground covered by weeds were made on sample quadrats; no significant differences were found between drilling distances in this respect, although on the plots sown with wild white clover, that plant provided a significantly higher proportion of ground cover on the wide drilled plots.

Of the smother crops, trefoil had the least effect, although it

Table II. *Yields of dry matter—cwts per acre*

	Widths of drilling						Smother crops					
	3½ in.	7 in.	10½ in.	14 in.	S.E. of a mean	Significance	Cocksfoot (C)	Wild white clover (W)	Trefoil (T)	Nothing (O)	S.E. of a mean	Significance
	May—June cuts											
29 May 1934	47·62	48·71	46·30	46·34	0·702	Insig.	57·15	44·57	44·55	42 72	0·692	C>W, T, O***
28 May 1935	49·84	48·13	47·61	45·38	0·952	Reg.**	59·37	43·75	44·59	43·26	0·860	C>W, T, O***
8 June 1936	34·42	32·51	33·23	32·62	1·194	Insig.	40·55	30·92	30·91	30·41	0·697	C>W, T, O***
9 June 1937	44·40	44·20	42·78	47·59	1·177	Insig.	56·06	43·05	39·40	40·45	0·748	C>W, T, O*** W>T** W>O*
4 years' total	176·28	173·55	169·92	171·93	2·379	Insig.	213·13	162·29	159·45	156·84	1·711	†Interaction** C>W, T, O*** W>O*
	July cuts											
23 July 1934	25·18	25 65	24·27	23·68	0·461	Reg.*	20·96	25·20	25·51	27·12	0·630	W, T, O>C*** O>W*
26 July 1935	30·30	29·95	29·48	28·32	0·483	Reg.**	32·40	28·72	28·67	28·25	0·432	C>W, T, O***
27 July 1936	31·16	31·78	30·49	29 10	0·659	Reg.*	31·22	30·51	30·35	30·45	0·629	Insig.
3 years' total	86·64	87·38	84·24	81·10	1·145	Reg.*	84·58	84·43	84·53	85·82	0·953	‡Interaction*
	August cuts											
28 Aug. 1935	8·42	8·54	8·56	8·36	0·228	Insig.	8·16	8·65	8·73	8·33	0·242	Insig.
24 Aug. 1936	9·13	8·65	8·08	7 73	0·184	Reg.***	9·18	8·01	8·22	8·18	0·227	C>W, T, O**
2 years' total	17·55	17·19	16·64	16·09	0·291	Reg.**	17·34	16·66	16·95	16·51	—	§Interaction*
Grand total of all cuts in the 4 years	280·47	278·12	270·80	269·12	3·205	Reg.*	315·05	263·38	260·93	259·17	1·874	C>W, T, O**
Ditto—rel. figs.	104·2	103·3	100·6	100·0	—	—	121·6	101 6	100·7	100·0	—	—

† Widest spacing easily best on O and W, not on C and T.
‡ 14 in. low except on cocksfoot plots—the interaction only just significant.
§ In wide rows wild white clover plots very low.

contributed 10% of the herbage cut from its plots in May 1934. No significance in total yield between the trefoil and other plots was found at that or at any other cut. Abnormally droughty conditions were experienced during the summer of 1934, and at the second cut of that season the plots sown with wild white clover gave yields slightly, but significantly, below those of the control plots. This might be attributed to the wild white clover leading to some reduction in the number of plants of lucerne during the first harvest year; some evidence of this is seen in Table 1, but the effect seems to have been transitory, and to have vanished by the second harvest year. The weed estimations made in 1937 showed that the proportion of the plots sown with wild white clover which was covered by weeds was significantly less than that on the control or on the trefoil plots. This probably explains the fact that at the June cut of that year the wild white clover plots significantly outyielded the control plots or the plots sown with trefoil. Thus it appears that although wild white clover may be slightly harmful to a lucerne stand in the early stages of a ley it is not so aggressive as the weeds which it suppresses in the later stages. It must be pointed out that the yield differences involved were small.

The cocksfoot grew vigorously throughout the ley, and analyses of herbage cut during May and June showed that its contribution was 40–60% of the material provided by the plots. In the dry summer of 1934 it made little aftermath growth, but in the wet summer of 1936 it grew vigorously during August when it contributed 40% of the total yield. At the spring cuts the cocksfoot plots yielded consistently higher than the others, the differences in all cases being large and highly significant. Cuts made later in the season gave results which were somewhat inconsistent, but only once did the cocksfoot plots yield significantly less than the others, and that was at the July cut of the dry season of 1934. Over the whole period cocksfoot plots outyielded the remainder by more than 20% (equivalent to nearly 3 tons of dry matter per acre). It is recognized that figures for dry matter yield do not necessarily give a true picture of yield of nutrients, but if cuts are made before, or at, early flowering stage (as was the case of this experiment) the mixture of cocksfoot and lucerne is very palatable and nutritious; the herbage is also somewhat easier to convert into hay than pure lucerne, and is admirable material for silage making. Cocksfoot almost completely controlled weeds, very few of which could be found on any of its plots, and at the conclusion of the experiment, when all the other plots carried little but weeds almost a pure culture of cocksfoot remained on the plots sown with that species.

SUMMARY

As a result of one detailed experiment and four demonstrations carried out on the University Farm at Cambridge the following conclusions can be drawn:

1. Lucerne drilled at a constant seed rate per acre, in narrow rows (3½ and 7 in.), gave a greater yield per acre than when drilled in rows 10½ and 14 in. in width. Over a four-year period the yield of dry matter per acre from narrow rows was half a ton more than from wide rows. No evidence was obtained that weed infestation is reduced by narrow drilling.

2. The broadcasting of 5 lb. of trefoil per acre at the time the lucerne was drilled had no effect on the total yield or on weed infestation.

3. Wild white clover broadcast at the rate of 2 lb. per acre at the time of drilling the lucerne slightly reduced the yield of lucerne in the first harvest year, but subsequently it served to secure some control of weeds, and thereby favoured the persistence of the lucerne. Differences in yield associated with sowing wild white clover were, however, slight.

4. Commercial cocksfoot broadcast at the rate of 10 lb. per acre at the time of drilling the lucerne led to very considerable increases in total yield (nearly 3 tons per acre of dry matter over a four-year period). The increments were obtained principally during the spring growth, and some loss of lucerne plants was suffered, so that in a very dry summer the total aftermath yield was slightly reduced. Since cocksfoot almost completely controlled weeds and its mixture with lucerne was very suitable for hay or for silage, it is regarded as a plant that may be included in a lucerne ley with advantage.

REFERENCES

BATES, G. H. (1935). *J. Minist. Agric.* **42**, 134.
McKAY, J. G. (1928). *N.Z.J. Agric.* **37**, 386.
PARKER, W. H. (1931). *J. nat. Inst. agric. Bot.* **3**, 111.
SPAFFORD, W. P. (1931). *J. Dep. Agric. S. Aust.* **34**, 927.

THE COMPOSITION AND NUTRITIVE VALUE, WHEN FED TO RUMINANTS, OF PEA-POD MEAL AND BROAD-BEAN-POD MEAL

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INTRODUCTION

THE possible shortage of imported feeding stuffs during war time demands that the fullest use should be made of home-grown foods and their by-products. Conspicuous among such by-products are the pea-pods that accumulate in large quantities at the factories during the pea-canning season. Preliminary analyses made by the writers some years ago suggested that such pea-pods, which at the time of canning are usually in a young and immature stage of development, might have considerable value as a food for live-stock. Different samples were found to contain from 78 to 83 % of moisture and, on the basis of dry matter, about 15 % of crude protein, 60–64 % of N-free extractives, 16–18 % of crude fibre and 5 6 % of ash, the last constituent containing approximately 1·5 % of CaO, 0·6 % of P_2O_5 and 0·3 % of Cl_2.

It is very desirable, therefore, that attention should be directed at the present time to the problem of the utilization of pea-pods, from the canning factories and elsewhere, in the feeding of farm animals. Since grass is usually plentiful during the period of the canning season, the best method of dealing with the pea-pods is to conserve them for use in winter-feeding, although a proportion might well be utilized in the fresh condition for feeding to sows, boars and bacon pigs (e.g. as in the Lehmann system of feeding), this method of disposal being particularly advantageous in connexion with pea-pods arising as a domestic by-product.

Pea-pods can best be conserved on the farm in the form of silage. This process, provided consolidation by trampling is carried out efficiently, gives rise to a very satisfactory product that is consumed readily by sheep and cattle. As made in tower silos, it is pale yellowish-green in colour and has a pleasant vinegary smell with little or no butyric acid. Indeed, the silage so made is reminiscent of the "acid-brown" type of

silage that can be obtained under certain conditions from the con-
servation of an oat and vetch crop. A sample analysed some years ago
by the writers contained 73·5% of moisture and, on the basis of dry
matter, 13·5% of crude protein, 54·7% of N-free extractives, 24·8% of
crude fibre, 5% of ash, 1·55% of CaO and 0·44% of P_2O_5. It is not
necessary to supplement the pea-pods during filling with molasses, a
favourable fermentation being ensured by the considerable proportion of
sugar that the pea-pods were shown to contain. Although up to the
present the writers' experience of making pea-pod silage is limited to
ensilage in tower silos, there can be little doubt that successful pre-
servation could be achieved in pits and small portable silos. Such silos,
however, should be provided with an efficient means of carrying away
effluent, since considerable volumes of liquid drain away from the ensiled
mass during the period in which filling is proceeding.

It should be pointed out that broad-bean-pods, on the other hand,
do not lend themselves to successful conservation by ensilage. They
become "slimy" during the process and give rise to an unpalatable
product. For this reason, resort must be had, for the conservation of
this by-product, to the method of artificial-drying, one form of which
is described below. Such artificial-drying is essentially a process to be
carried out by the canning factory itself.

At the Huntingdon Canning Factory of Messrs Chivers and Sons, Ltd.,
the artificial-drying of the pea-pods and broad-bean-pods is carried out
as follows: It should be observed in the first place that the bean-pods,
owing to their tendency in the wet state to turn black after a very short
time, are always given preference over the pea-pods in the drying process,
the drier being kept at full working capacity by the addition, if necessary,
of the requisite proportion of pea-pods. When bean-pods are available
for drying, therefore, the resultant dried product usually consists of a
mixture of dried bean-pods and dried pea-pods. Any surplus of pea-pods
beyond the capacity of the drier at such times passes on by means of
a mechanical conveyor to the top of a neighbouring tall, concrete,
cylindrical tower silo and is converted into silage.

The drying appliance is a Dunford and Elliott drier. It consists
essentially of two large drums, each 17 ft. in length and 11 ft. in diameter,
one of which is placed at a somewhat higher level than the other, and
each provided with vanes that keep the pods agitated during the drying
process. The drums revolve slowly in the same direction at the rate of
one revolution per minute. The hot fumes from anthracite kilns are
drawn through the drums by means of a fan.

The pods are fed at a controlled rate into the higher drum. For bean-pods, the temperature of the inlet gases is about 450° F. and for pea-pods about 420° F. During the drying operation the pods "overflow" slowly and continuously into the second and lower drum, where the temperature of the hot gases is about 250° F. At this stage the pods are about half-dry, the process being completed in the lower drum. The total drying time is about 6 hr., the pods remaining roughly 3 hr. in each drum. During the process they lose entirely their green colour and the final product is obtained, after milling, as a fine, brown meal, which is a suitable form for transport and for inclusion in compound meals and cubes. The process of milling and bagging is carried out in an adjacent room to remove the danger of the fine dust catching fire.

The yield of dried meal is 3–4 cwt. per hr. This rate of drying, considering the size and nature of the drying plant, may seem unimpressive, but it must be borne in mind that the drying of such wet pods could never be such a quick and straightforward process as is the drying of green crops such as grass and lucerne. The major consideration from the factory standpoint is the disposal of a by-product that would otherwise accumulate and putrefy.

COMPOSITION OF PEA-POD MEAL AND BROAD-BEAN-POD MEAL

For the purposes of the present trials it was arranged to secure pure grades of the pea-pod and bean-pod meals. The investigation was restricted to the examination of the chemical composition of the dried meals and their digestibility and nutritive value when fed to sheep. It is

Table I. *Composition of pea-pod meal and bean-pod meal on the basis of dry matter*

	Pea-pod meal %		Bean-pod meal %	
Crude protein	14·97		16·62	
Ether extract	1·33		1·12	
N-free extractives	60·21		57·16	
Crude fibre	17·18		17·82	
Ash	6·31		7·28	
Lime (CaO)	1·52		0·92	
Phosphoric acid (P_2O_5)	0·60		0·60	
Potash (K_2O)	1·47		2·60	
Soda (Na_2O)	0·21		0·54	
Chlorine (Cl_2)	0·35		0·52	
True protein	9·03		12·13	
"Amides"	5·94		4·49	
Sucrose	8·83	16·53	2·90	6·43
Invert sugar	7·70		3·53	
Moisture in meals as received from factory	9·30		7·50	

intended shortly to extend the work in the direction of investigating the digestibility and feeding value of the meals in the nutrition of the bacon pig and of fresh pea-pods, pea-pod silage and pea-haulm silage (which can be made very successfully in large stacks) in the feeding of both pigs and ruminants.

Comments on Table I

The figures are for the most part self-explanatory. It may be pointed out, however, that the pea-pod meal, in some respects, particularly in regard to its satisfactory content of protein and lime, has a composition not unlike that of the leguminous hays. This is brought out by the comparison between pea-pod meal and red clover hay shown in Table II. The similarity, however, does not extend to the fibrous constituent, pea-pod meal having a very much lower fibre content than the hay. Although the present consignment of pea-pod meal was very much poorer in lime and somewhat less rich in crude protein than lucerne meal (see Table II), it compared very favourably in other respects, particularly in regard to its much lower fibre content.

Table II. *Comparison of pea-pod meal with red clover hay*
and lucerne meal (dry-matter basis)

	Crude protein %	Crude fibre %	Ash %	Lime %	Phosphoric acid %	Chlorine %
Pea-pod meal	14·97	17·18	6·31	1·52	0·60	0·35
Red clover hay*	16·17	28·74	7·19	1·64	0·41	0·25
Lucerne meal†	17·82	26·93	11·21	3·98	0·45	0·52

* Wood & Woodman, 1939.
† Artificially-dried lucerne from 2nd cut in early flower (Woodman & Eden, 1935).

An outstanding characteristic of pea-pod meal is the richness of this product in sugar, no less than 16·5% of the dry matter consisting of a mixture of sucrose and invert sugar. It is the presence of this abundance of sugar that accounts for the favourable fermentation that takes place when young pea-pods in the fresh condition are conserved as silage.

It will be observed that bean-pod meal displays the same general features in respect of chemical composition. The consignment used in this investigation, however, was slightly richer in crude protein, but distinctly poorer in lime and sugar, than the pea-pod meal. In both products a substantial proportion of the crude protein was present in the form of non-protein nitrogenous substances.

In view of the importance attributed to the carotene content of such

artificially-dried green fodders as lucerne meal and dried young grass, it was considered desirable to determine the amounts of carotene and xanthophyll in the pea-pods and bean-pods both before and after drying. Indeed, the attention of the writers was first drawn to these products by inquiries as to their suitability as a source of carotene in pig-feeding. The determinations were carried out by the method described by Ferguson & Bishop (1936) and the results are shown in Table III.

Table III. *Carotene and xanthophyll content of fresh and artificially-dried pea-pods and bean-pods*

	Carotene mg. per 100 g. dry matter	Xanthophyll mg. per 100 g. dry matter
{Fresh pea-pods	2·4	4·5
{Pea-pod meal	2·6	4·2
{Fresh bean pods	3·5	9·3
{Bean-pod meal	3·4	6·9

It will be seen from the figures in Table III that pea-pods and bean-pods, both in the fresh and artificially-dried states, have little or no significance as a source of carotene in the feeding of live-stock. The amount of this pigment in these feeding products is very small (compare with grass, which contains 30–60 mg. of carotene per 100 g. dry matter). It is of interest to note, however, that the small amount of carotene in the fresh pods is still contained in the dried products, despite the lengthy nature of the drying process and the high temperature of the drying gases. This finding is a further demonstration that, provided the drying is carried out in a non-oxidizing atmosphere, in this case ensured by the hot fumes from the anthracite kilns, little destruction of carotene need result from the artificial-drying of such green crops as lucerne and grass.

RESULTS OF DIGESTION TRIALS

Two wether sheep (Border Leicester × Cheviot ewe crossed with Suffolk ram) were used in the digestion trials. They were about 17 months old and weighed 143 and 141 lb. respectively at the beginning of the trials in September 1938.

The sheep were brought from grass and accustomed to a ration of chaffed meadow hay. After some days on this diet, a small allowance of pea-pod meal was introduced into the ration. Despite the sweet and appetizing smell of the meal, however, it was not found possible to induce the animals to eat it in this form, a difficulty that was at first attributed to its dry and dusty nature. Subsequent tests, in which the meal was

13–2

damped with water, were equally unsuccessful, although the addition of the water distinctly intensified the sweetish smell. The conclusion could not be avoided that the pea-pod meal was unpalatable. When a little was placed on the tongue, the initial sensation was one of slight sweetness, but this soon gave way to a distinctly bitter taste.

The difficulty was overcome by feeding the pea-pod meal in conjunction with a proportion of locust bean. The mixture was prepared in the following way: 700 g. of the pea-pod (or bean-pod) meal was mixed thoroughly with 280 c.c. of water, and 300 g. of kibbled locust bean was then stirred in to give a uniform mixture. The added water was completely taken up by the meal and the resultant mixture was pleasantly damp to the touch, having a friable appearance and being in a very suitable form for feeding purposes. The sheep quickly became accustomed to the meal as prepared in this way and ate the allowances readily and completely.

It is clear, however, that artificially-dried pea-pod meal has, when fed alone, a low palatability and would best be utilized for feeding as a constituent of a compound feeding meal or cube supplying a further ingredient for the purpose of ensuring tastiness and palatability. This disadvantage, however, does not attach to pea-pods when converted into silage, a process that would naturally recommend itself to the farmer who wished to conserve this by-product for use in winter-feeding. It is possible that farmers delivering peas to the factory might take pea-pods back to the farm for the purpose of ensilage.

The daily ration in period 1 consisted of 700 g. of pea-pod meal and 300 g. of kibbled locust bean, made up with 280 c.c. of water, together with an allowance of 400 g. of chaffed meadow hay. The digestibility of the bean-pod meal was determined in like manner during period 2, the 700 g. of pea-pod meal being replaced by an equal weight of bean-pod meal. The final period was devoted to the measurement of the digestibility of the basal food, the daily ration consisting of 800 g. of chaffed meadow hay and 600 g. of kibbled locust bean.

The composition of the pea-pod meal and bean-pod meal has been recorded already in Table I. The meadow hay contained, on the basis of dry matter, 9·29% of crude protein, 3·90% of ether extract, 49·51% of N-free extractives, 30·36% of crude fibre and 6·94% of ash. Since very few analyses of locust bean meal have been made in this country, attention was paid to securing full details about the composition of the sample used in these trials. According to the merchant who supplied the product, 75% of the seeds had been removed after kibbling, so that

the kibbled locust bean as analysed and fed contained 25% of the hard seeds, mostly in the unbroken condition. The results of the analysis are shown in Table IV. It will be noted that the total sugar content of the sample is rather higher than the figure usually recorded in the literature.

Table IV. *Composition of kibbled locust bean (dry-matter basis)*

Crude protein %	Ether extract %	N-free extractives %	Crude fibre %	Ash %	Lime %	Phosphoric acid %	Potash %
4·20	0·76	83·63	8·38	3 03	0·60	0 15	1·11

Soda %	Chlorine %	True protein %	"Amides" %	Sucrose %	Invert sugar %	Total sugar %
0·16	0·23	2·97	1·23	35·84	13·01	48·85

The digestion coefficients (mean for two sheep) of the pea-pod meal and bean-pod meal, as well as the results for the basal ration, are recorded in Table V. The complete figures necessary for the calculation of the digestion coefficients are summarized in the appendix to this paper.

Table V. *Summary of digestion coefficients*

	Pea-pod meal %	Bean-pod meal %	Basal ration (meadow hay plus kibbled locust bean) %
Dry matter	66·7	65·2	52·0
Organic matter	68·4	65·9	53·1
Crude protein*	42·5	31·8	16·2
Ether extract	70·5	55·2	57·7
N-free extractives	76·6	78·4	62·5
Crude fibre	61·9	58·2	36·2
By *in vitro* method	72·3	67·2	{72·1 (meadow hay) {60·4 (locust bean)

Comments on Table V

It will be observed that pea-pod meal · has a very satisfactory digestibility, roughly two-thirds of the food material which it contains being capable of digestion by ruminants. In particular, about three-quarters of the N-free extractives, which form about 60% of the total dry substance of the meal and of which rather more than one-quarter is in the form of sugar, is digestible. That the process of lignification has not proceeded far in the young pea-pods as separated in the canning industry is apparent from the magnitude of the digestion coefficient of the fibrous component, namely, 61·9%. It will further be noted that, in respect of digestibility, pea-pod meal and bean-pod meal are very similar.

The low values for the digestion coefficient of the crude protein of the pea-pod meal (42·5%) and of the bean-pod meal (31·8%) are, at

first sight, somewhat unexpected, since determinations by the pepsin-HCl method gave the much higher values of 72·3 and 67·2% respectively. A consideration of the evidence leads to the conclusion that the locust bean, which was incorporated in the diets with the object of improving palatability, caused a very distinct depression in the extent to which the protein of the rations could be digested. A very striking depression was also noted in the basal period, when the diet composed of 800 g. of meadow hay and 600 g. of kibbled locust bean was tested. In this case, separate *in vitro* determinations of the digestion coefficients of the protein in the meadow hay and locust bean gave the values 72·1 and 60·4% respectively, whereas the value from the sheep trial for the mixed protein in the basal diet was as low as 16·2%.

The depressing influence of locust bean on protein digestibility is to be attributed to its high sugar content, which amounted to nearly 50% of the dry matter. It is a finding that should be given serious consideration by farmers who regularly use locust bean meal for enhancing the palatability of rations and by manufacturers who are in the habit of incorporating this feeding product in compound foods. As a food for inclusion in experimental diets, when the purpose in view is the measurement of the digestibility of one of the ingredients of the ration, locust bean meal is entirely unsatisfactory.

Table VI. *Digestible composition and nutritive value of pea-pod meal and bean-pod meal (dry-matter basis)*

	Pea-pod meal %	Bean-pod meal %
Digestible crude protein*	10·82	11·17
Digestible ether extract	0·94	0·62
Digestible N-free extractives	46·12	44·81
Digestible fibre	10·63	10·37
Digestible total organic matter	68·51	66·97
Digestible true protein	4·88	6·68
Protein equivalent	7·85	8·93
Starch equivalent†	30·94	59·58

* Using the digestion coefficient of the crude protein as determined by the *in vitro* method.

† Using the fibre correction factor 0·29, because (1) the food is in the form of meal and (2) the fibre content calculated to the basis of fresh pea-pods and bean-pods (18·0 and 13·6% dry matter respectively) is less than 4%.

Comments on Table VI

The values for the starch equivalent and protein equivalent of the pea-pod meal and bean-pod meal are calculated in Table VII to a 10% moisture basis and are compared with the corresponding values for meadow hay and red clover hay (Wood & Woodman, 1939).

Table VII. *Nutritive value of pea-pod meal and bean-pod meal compared with that of meadow hay and red clover hay*

	Moisture content %	Starch equivalent %	Protein equivalent %
Pea-pod meal	10·0	54·8	7·1
Bean-pod meal	10·0	53·6	8·0
Meadow hay (medium grade)	14·3	37·0	4·6
Meadow hay (best grade)	16·0	48·0	7·8
Red clover hay (medium grade)	16·5	38·0	7·0
Red clover hay (best grade)	16·5	43·0	8·8

That pea-pod meal and bean-pod meal are to be regarded as valuable foods for sheep and cattle is at once apparent from the figures in Table VII. Taking medium meadow hay as the standard of comparison, pea-pod meal is roughly one-and-a-half times as rich in starch equivalent and protein equivalent. Bean-pod meal also displays a similar superiority over medium meadow hay. Indeed, both meals are superior, in respect of starch equivalent, to the *best* grade of hay made from grass or such leguminous crops as red clover. An additional comparison may be made with lucerne. The best sample of lucerne hay made by the writers during a number of years of work on the lucerne crop was found to have a moisture content of 16% and a starch equivalent of 37·1 (Woodman & Eden, 1935), a value that falls well below the figures for both pea-pod and bean-pod meal. The higher protein equivalent for the lucerne hay (11·9%) should, however, be noted.

The following examples of rations containing dried pea-pods have been computed in order to give a more concrete impression of the feeding value of this product:

(1) To fatten a store beast of 8 cwt. live-weight at the rate of 2 lb. live-weight increase per day. Required: a ration supplying 10 lb. of starch equivalent, including 1·5 lb. digestible protein, in a bulk of not more than 20·5 lb. of dry matter.

	Dry matter lb.	Starch equivalent lb.	Digestible protein lb.
7 lb. dried pea-pods	6·3	3·84	0·50*
6 lb. oat straw	5·2	1·20	0·06
50 lb. swedes	5·8	3·65	0·35*
1 lb. crushed beans	0·9	0·66	0·20
1 lb. dec. ground nut cake	0·9	0·73	0·42
Total†	19·1	10·08	1·53

* Based on protein equivalent.
† It will be noted that the above ration contains neither hay nor cereal grain.

(2) Dairy cow of 10–11 cwt. live-weight (maintenance plus first gallon). Required: a ration supplying 9–9·5 lb. starch equivalent including about 1·3 lb. digestible protein.

	Starch equivalent lb.	Digestible protein lb.
14 lb. dried pea-pods	7·67	1·00
5 lb. medium meadow hay	1·85	0·27
Total	9·52	1·27

(3) Production ration per gallon of milk (3·7% fat). Required: an amount of food supplying 2·5 lb. starch equivalent including about 0·6 lb. digestible protein.

	Starch equivalent lb.	Digestible protein lb.
2 lb. dried pea-pods	1·096	0·142
1 lb. crushed barley	0·714	0·076
1 lb. dec. ground nut cake	0·730	0·420
Total*	2·540	0·638

* This production mixture should be used at the rate of 4 lb. per gallon of milk. The utilization of dried pea-pods for this purpose would enable a saving of 3·5 − 2 = 1·5 lb. of concentrates to be made in the production of a gallon of milk.

During the coming pea-canning season, the writers intend to investigate the digestibility and nutritive value of fresh pea-pods and pea-pod silage. It is in this latter form, rather than in the form of dried pea-pods, that the farmer is likely to utilize this by-product in winter-feeding. It may be assumed provisionally that 7 lb. of dried pea-pods (10% moisture) are equivalent approximately to 35 lb. of fresh pea-pods (82% moisture) or to 25–30 lb. of pea-pod silage (75% moisture).

SUMMARY

Attention is directed in this paper to the desirability, particularly at the present time, of conserving, for purposes of winter-feeding, the pea-pods that accumulate in large quantities at the factories during the pea-canning season. Conservation on the farm is best carried out by the method of ensilage, young pea-pods, such as are obtained in the factory, giving rise to a very satisfactory type of silage without the use of molasses. Broad-bean-pods, on the other hand, do not lend themselves to successful conservation by ensilage, owing to the fact that they become "slimy" in the process and yield an unpalatable product.

Both pea-pods and bean-pods are conserved in the factory by the method of artificial-drying. One such process is described in the present paper. The final product in both cases is obtained as a fine brown meal.

Pea-pod meal, in some respects, particularly in regard to its satisfactory content of protein and lime, has a composition not unlike that of the leguminous hays. The similarity, however, does not extend to the fibrous constituent, pea-pod meal having a very much lower fibre content than the hays.

An outstanding characteristic of pea-pod meal is its richness in sugar, no less than 16·5 % of the dry matter consisting of a mixture of sucrose and invert sugar. It is the presence of this abundance of sugar that accounts for the favourable fermentation that takes place when young pea-pods in the fresh condition are conserved as silage.

Bean-pod meal displays the same general features in respect of composition, but is distinctly poorer in lime and sugar than the pea-pod meal. Pea-pods and bean-pods, both in the fresh and artificially-dried condition, contain very little carotene and have, therefore, little or no significance as a source of this vitamin A-precursor in the feeding of live-stock.

Pea-pod meal, when fed alone, has a low palatability and would best be utilized for feeding as a constituent of a compound meal or cube supplying a further ingredient to ensure tastiness. This disadvantage does not attach to pea-pod silage. In the present digestion trials, the pea-pod meal and the bean-pod meal were rendered palatable by admixture with kibbled locust bean. The depressing effect of the locust bean, on account of its high sugar content, on protein digestibility is well illustrated by the results of these trials, and attention is directed to the practical consequences of this finding.

Both pea-pod meal and bean-pod meal have a very satisfactory digestibility, roughly two-thirds of the food material which they contain being capable of digestion by ruminants. On the basis of a 10% moisture content, pea-pod meal contains 54·8% of starch equivalent, including 7·1 % of protein equivalent, the corresponding values for bean-pod meal being 53·6 and 8·0%. Pea-pod meal is roughly one-and-a-half times as rich as medium meadow hay in starch equivalent and protein equivalent, and both meals are superior, in respect of starch equivalent, to the *best* grade of hay made from grass or leguminous crops. Examples of rations containing dried pea-pods have been computed to illustrate the considerable saving of hay and concentrates that becomes possible when this by-product, or pea-pod silage, is used in winter dietaries.

In conclusion, the writers desire to express their gratitude to G. E. Govier, Esq., of Messrs Chivers and Sons, Ltd. (Huntingdon Canning

A STUDY OF FECUNDITY IN THE DOMESTIC FOWL: THE BEHAVIOUR OF PERSISTENCY IN INDIVIDUAL HENS

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(With One Text-figure)

INTRODUCTION

AMONG the investigations that have been undertaken in the search for measurable inherited traits related to fecundity in the fowl, persistency of production is a character which has commanded considerable attention. Basing their views on family behaviour, Goodale & Sanborn (1922) suggested that the cessation of egg production in the autumn and late summer of the pullet year, associated with the annual moulting and replacement of the plumage, has a genetic foundation.

Hurst (1925) postulated that early complete moult (with coincident termination of egg-laying) depended on the action of a single dominant Mendelian factor. On the other hand, Hays (1936) concluded from a statistical study of three generations of Rhode Island Red fowls that high persistency, as measured by the number of days from the first egg in autumn to the onset of the moult in the following year, was likewise controlled by a single dominant gene. In an analysis of the relation of a number of variables involved in pullet year production, Knox *et al.* (1935) measured persistency as the number of eggs laid in the last 50 days of a 365-day period from the onset of production, and also by the number laid in August and September.

All the various workers are agreed as to the heritable nature of persistency, but it is evident that the units by which they seek to measure this character differ considerably and this renders comparison of results difficult. It is therefore not entirely surprising that Hurst, using the date of the moult, and Hays, the length of the antecedent laying period, should have arrived at a directly opposite conclusion as to the mode of its inheritance.

As suggested by Taylor & Lerner (1938), it is clear that for future

studies on this problem a more precise definition of persistency is required, together with an appreciation of the relation or otherwise of the units already in use. Obviously the date of the last egg produced at the end of the pullet year, and the length of the laying period could only be analogous units if onset of production occurred at the same time in all birds, which it does not. The figures of Knox *et al.* deal with the last part of the cycle only but involve the rate of egg production as well as the length of the laying period. Even if the former could be disregarded, the August and September measurement would be comparable with the date of last egg only if the moult commenced in all birds within the limits of these two months, while their 50-day period does not take the date of the moult into consideration at all. It is necessary to emphasize these differences for they must be borne in mind in discussing the data presented here.

Starting from the premise that persistency of production, as determined by the date of last egg, is an inherited phenomenon, observations collected over a number of years on the Institute's flock of Brown Leghorns have been analysed in an attempt to determine the intensity of genetic control of a physiological process known to be susceptible to extraneous environmental influences. The idea that such analysis might yield some useful information was first suggested by an inspection of data provided by aged hens. Where moulting dates of individuals were available over several years there appeared to be a tendency in particular hens for such dates to coincide, giving the impression that each bird had a characteristic date on which she produced the last egg of a laying cycle. The most striking example met with is provided by the oldest female in our flock: she is now in her 10th year, and in successive years from 1931 to 1938 her production cycles terminated on 17, 17, 3, 22, 18, 12, 10 and 20 October respectively.

MATERIAL

In the years covered by the observations all birds have been kept strictly intensively, and with the exception of a reduction of the maize content in the grain ration during the summer months, and the addition of a wet mash feed in the winter, the method of husbandry has been kept constant. Electric lighting of all pens is used in the winter months until 6 p.m.

For two reasons it was found necessary to omit the observations on certain members of the population. In the first place, specific experiments

interfered with normal productivity, and secondly, some birds were removed from one pen to another in the late summer or early autumn period. Although the onset of the moult takes place somewhat suddenly it has been found, by determining experimentally the rate of feather replacement in plucked areas on the body of the hen, that conditions leading up to it are acquired gradually. It commonly happens that birds roughly handled or moved from pen to pen at this time of the year enter the moult prematurely.

Altogether observations on the date of cessation of egg production in 269 birds at the end of the pullet and second laying year have been analysed, while for 3 years' behaviour 129 birds were available. The hens were hatched over a number of years so that abnormal climatic effects will be randomized and not coincide with age classes.

RESULTS

A wide variation is found in the time at which birds produce the last egg of the laying cycle and all months from July to December are involved (Table 1). The actual spread in time was from 22 July to 31 December (163 days) for pullets, and from 6 July to 22 December (170 days) for the same birds at the end of the second year of production.

Table I. *Variation in time of last egg by calendar months for the same birds in their first and second years*

Month	Number of birds	
	1st year	2nd year
July	1	5
August	7	13
September	91	92
October	127	112
November	31	36
December	12	11
Population	269	269

The majority of the birds cease laying and enter the moulting phase in September and October in both years, but there appears to be a tendency to moult somewhat earlier in the second year as shown by the calculated mean difference of -5.97 ± 1.74 days between dates of last eggs in the two successive cycles. There are no suggestions of subsidiary peaks in the frequency curves for the 2 years, however, and the data might well represent a tendency for all birds to moult at a definite seasonal point, say, the beginning of October.

When the proximity of first and second year moulting dates in individuals is examined, those showing a divergence of not more than 6 days were found to constitute a quarter of the population (Fig. 1). The unit, 6 days, was chosen quite arbitrarily, but it seems reasonable

Population: 269 birds
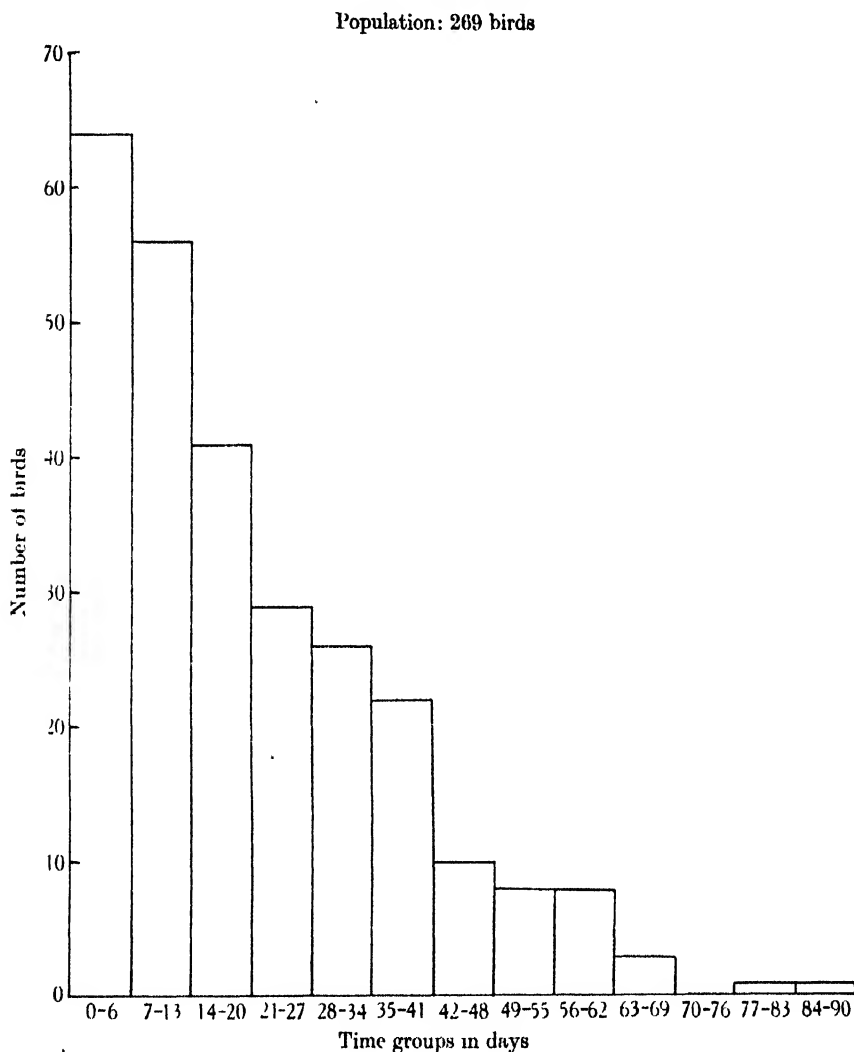
Fig. 1. Variation in time interval between end of first and second production cycles.

to consider that the majority of those closely similar pairings approximate to the inherent moulting date of the individual practically freed from external modification. If then, there were a fixed seasonal time for the moult it would be expected that this class showing close similarity in successive terminal dates would be grouped together near the time when

the greatest number of birds cease production. Actually the same percentage of individuals shows this close relationship for each of the months in which a sufficient number of observations are available, viz. September 24·4%, October 24·6%, and November 25·8%. The data not only support the conclusions of previous workers on the presence of genetic control, but also yield a suggestion of its complexity and spread, for not only are birds, expressing apparently inherent moulting dates, present in each of these three months, but it is easy to deduce that the number of birds in the more extreme groups (i.e. July, August and December) which show the same close approximation in terminal dates in successive years must also be in the region of a quarter of their total.

From the brief analysis of the observations drawn from this population it is clear that the date of last egg at the end of the pullet year cannot be regarded as a reliable expression of an inherent individual tendency since, when the behaviour over two years is considered, a relatively small percentage of birds reproduces a similar termination of the cycle: 75% show a difference of more than 6 days in successive years while more than half give a difference greater than 13 days. Even the data from two years are of little more value in defining the character, for although the cessation of egg production was 6 days earlier on the average in the second year, only 64% of individuals actually ceased earlier than their first year date while 30% were later. Thus, where wide differences in the two years' dates are found there is no indication which of these approaches more closely the inherent locus, and the tendency to moult earlier in the second year is disguised in individuals by other variations.

Analysis of the data from 129 birds observed over three laying cycles shows that between the date of last egg in the pullet year and that of the third, thirty-three birds or 25·6% fall within the 6-day group, while between the pullet and second year thirty-four birds or 26·3% of this population behave similarly; between the second and third the number of birds is thirty or 23·2%. The interesting point arising from these figures is that although approximately the same number of birds show a close similarity in date when any 2 of the 3 years' observations are considered, the same individuals are not necessarily involved, for only 10·8% had all three dates falling within the 6-day group, while sixty-nine birds or 54% had two out of three terminal dates showing as small a difference. Thus there are not sufficient grounds for suggesting that birds with closely similar terminal dates possess a superior genetic control of the phenomenon or show a greater resistance to the operation of environmental factors.

It has been assumed that where the dates of cessation of egg production in any 2 years are close together they may be taken as approximating to the inherent individual date. Individuals exhibiting this close relationship show a wide variation in time, occurring in all months from August to December, and on this postulation must be regarded as representing a large number of phenotypes arising from the action of several genetic factors. This assumption however is in contradiction to the genetic situations postulated by Hurst (1925) and Hays (1936). It is essential, therefore, to examine further the significance of these closely adjacent dates in individuals.

If the birds are not exhibiting specific phenotypes, the alternative view is that both dates are being modified by extraneous forces in the same way and to much the same extent. Such modifications, however, would be expected to take the form of inducing the termination of the egg laying cycle *earlier*. When the records for 3 years are studied the majority of birds (70%) show the similar dates occurring *later* than the atypical one.

Another method of approaching the question is to analyse the variance in the 3 years with respect to birds and to age. From Table II it can be

Table II. *Analysis of variance in the date of last egg*

Source of variation	D.F.	Sum of squares	Mean square	F	Significance of F (1% point)
Total	386	2741·308	7·102	—	—
Between birds	128	1837·308	14·354	4·583	1·42
Between ages	2	102·083	51·047	16·299	6·70
Error	256	801·917	3·132		

seen that a highly significant amount of variance is due to individuals. (It may be noted in passing that age is also a significant factor in the variance, a point which was suggested earlier by the consideration of the mean difference between dates of last egg in the first two years of production.) If genetic factors in the population act at points widely scattered in time, and the variance due to birds is indeed an indication of the dispersal of these genetic loci, then the elimination from the group of those birds with closely similar dates should not markedly lower the significance of individual variation. If, on the other hand, the number of genetic classes is small, or they fall within a limited period in the autumn months, we would expect the residual variance to be different following this elimination, for then a proportion of the closely paired terminal dates, which help to emphasize the importance of individual

behaviour, would be giving a false impression of the extent of genetic
control. For example, if all the genetic classes fell in October and
November, those paired dates occurring in August and September could
only be explained on the basis of extraneous forces affecting to the same
extent in different years the expression of the true genetic date, although
their behaviour of itself suggests direct genetic action. Thus in such cases
the elimination of these birds from the calculation of variance would
tend to remove the weighting of false individual loci and make more
evident the part played by forces other than genetic.

Table III. *Abstract of analyses of variance in date of last egg with
respect to birds and to age. Variance due to birds*

	F	Significance of F 1% point
Total population: 129 birds for 3 years	4·583	1·42
Eliminating birds with all 3 dates within 6 days: population 116 birds	4·258	1·42
Eliminating birds with all 3 dates within 20 days: population 69 birds	3·006	1·59
Eliminating birds with 2 out of 3 dates within 6 days: population 60 birds	3·450	1·73
Eliminating birds with 2 out of 3 dates within 13 days: population 21 birds	7·775	2·37

Further analyses of variance were therefore computed after removing
from the population birds with dates in either 2 or 3 years within 6, 13, or
even more days of one another; the percentage of birds with two out
of three dates within 13 days was so high (83·7 %) that further elimination
in this group was impracticable. Figures for variances due to individuals,
obtained in the selected groups, are shown in the abstract of the results
presented in Table III; their significance gives no indication of becoming
markedly reduced in the absence of the more consistently behaving
individuals. The range of environmental variation appears to be fairly
completely enclosed by the range of genetic variation, and there seem
to be no grounds for revising our original premise that closely similar
dates of cessation of egg production in different years represent an
approximation to an inherent tendency. Thus we are led to the conclusion
that either the date of last egg is dependent on a multiple factor situation,
or that the genes involved, though relatively stable in the individual,
show a considerable range of expression between birds.

SUMMARY AND CONCLUSIONS

1. Individual birds have a characteristic date for the termination of the egg laying cycle.

2. The date of cessation of production at the end of the pullet year is not a reliable indication of the bird's potentiality in this respect.

3. The longer the birds are retained the greater is the chance of distinguishing the true date.

4. Individual dates for the termination of the cycle occur at so many points throughout the total range (from July to December) that this must either indicate a multiple factor situation or that the genes involved show a considerable range of expression.

REFERENCES

GOODALE, H. D. & SANBORN, R. (1922). *Bull. Mass. agric. Exp. Sta.* no. 211.

HAYS, F. A. (1936). *Genetics*, **21**, 519–24.

HURST, C. C. (1925). *Experiments in Genetics*. Cambridge.

KNOX, C. W., JULL, M. A. & QUIN, J. P. (1935). *J. agric. Res.* **50**, 573–89.

TAYLOR, L. W. & LERNER, I. M. (1938). *Bull. Calif. agric. Exp. Sta.* no. 626.

THE DETERMINATION OF THE SIZE DISTRIBUTION OF SOIL CLODS AND CRUMBS

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MANY methods have been devised during the last twelve years to determine the size distribution of the clods or aggregates of the soil existing in the field, but there has been little study of their relative advantages and limitations, and research workers are therefore without guidance as to the most suitable method of structural analysis to use for a particular problem.

This gap is examined in the present paper, which is concerned only with the main types of methods available for determining the size distribution of the soil clods and crumbs and not with any detailed review of the literature, since this has recently been given by Russell (1938).

A distinction will be made between soil clods and soil crumbs. Clods will be defined as those soil aggregates or lumps that exist as isolated entities in the field; they may vary in size from large blocks a foot or so across down to fine dust. Since soil clods have only an ephemeral existence in the cultivated layer of an arable soil, a search has been made for some more fundamental structural unit. There is no experimental evidence yet for any fundamental aggregate entities in the soil such as the ultimate structural units postulated by Bouyoucos (1929), but by degrees the concept of water-stable aggregates has been built up, and although the size of these aggregates depends on the way the soil is wetted, the concept has proved extremely useful for experimental work. These water-stable soil aggregates will be called soil crumbs.

This paper is concerned with the determination of the size distribution of soil clods and soil crumbs, under the realization that these distributions are not absolute soil properties but depend on the experimental technique used. The choice of technique to be employed will thus be controlled by the use to which the determinations are to be put.

ANALYSIS OF THE FIELD STRUCTURE OF SOILS

The problem here is to find the size distribution of the clods that form the surface of the soil in the field. In all the methods in use a sample of the field soil is sieved on a bank of sieves and the weight of

soil on each sieve determined. These methods all assume that the aggregates found on the sieves actually exist in the field, an assumption that is certainly valid for many soil conditions, but is an unproven hypothesis for others. The fundamental technical difficulty is to get each clod on to its proper sieve, without breaking up the weak clods in the process. This former condition becomes very difficult to fulfil if the soil is too wet, for then the finer clods often stick together, forming a weakly coherent mass on a sieve through which they ought to pass.

The simplest technique, and the one in use at Rothamsted, has been described by Keen (1933). The banks of sieves used have a diameter of 16 in. and consist of four sieves and a bottom. The first three sieves are wire-woven and have apertures of $1\frac{1}{2}$, $\frac{5}{8}$ and $\frac{1}{4}$ in. respectively (about 38, 16 and 6 mm.), while the fourth is a brass sheet in which circular holes 3 mm. in diameter have been punched. A spadeful of soil is carefully taken and put on the top of the bank. No attempt is made to follow Puchner's (1911) technique and take a sample of known volume, as the Rothamsted soil is too stony to make this worth while. The bank is then gently sieved, and as each sieve seems finished it is taken off and the contents weighed.

The weight of the sample sieved is usually between 5 and 10 lb., but the weight on an individual sieve should not exceed 3 lb., otherwise efficient sieving becomes very difficult. A Salter spring balance graduated in half-ounces for weighing the fractions has been used, though a good balance weighing to ounces would probably be adequate. If an ordinary kitchen spring scale is used it must be carefully checked for accuracy as the cheap ones may easily have errors up to 4 oz. over parts of their scale.

This method yields reasonably reproducible results provided the soil is not too wet and the sieving is carried out properly. The results depend somewhat on the person sieving as is shown in Table I, which gives the mean results for three sieving teams which took a large number of samples from the same field on the same day.

Table 1. *The personal equation in field sieving*

	Percentage of soil on the sieve		
Sieve size	Team 1	Team 2	Team 3
$1\frac{1}{2}$ in.	15·5	9·6	11·6
$\frac{5}{8}$ in.	17·9	14·1	20·9
$\frac{1}{4}$ in.	16·5	17·0	25·3
3 mm.	25·4	26·6	31·6
Passing 3 mm.	24·7	32·6	10·7

In this example Team 2 consistently sieved more vigorously than Team 1, yet both were sieving efficiently and their results had equal value as judged by other criteria. On the other hand Team 3, judged by these same criteria, sieved inefficiently and their results were so erratic that they had to be ignored. This team was not in fact properly trained and had no adequate supervision. The personal factor can probably be eliminated by shaking the sieves mechanically in some machine, such as Volkov's (1933), which gives them a standard jolt. This method has not been tried here yet, on the grounds that the additional information obtained would not be commensurate with the inconveniences which it would introduce into the field work.

If the soil is too wet the method fails, as already stated, because many small crumbs that should pass the 3 mm. sieve stick together as they are being rolled over the sieve and form loose aggregates on it. The trouble, which may also occur to a smaller extent on the $\frac{1}{4}$ in. sieve, is aggravated by overloading the sieves, and in fact if the soil is rather sticky, the loads on the $\frac{1}{4}$ in. and the 3 mm. sieves should be well under 2 lb. Fortunately it is always obvious during sieving if the soil is wet enough to make this trouble serious.

Two methods have been tried to overcome this difficulty. The soil sample can first be air-dried as suggested by Mangelsdorff (1929), or at least partially dried; or the wet soil can be sieved in some inert liquid in which the lumps neither slake nor stick together.

The effect of drying the sample on its aggregate distribution is complex, since drying seems, to strengthen some clods and weaken others. Table II gives an illustration of this. The arable soil used was

Table 11. *The effect of moisture content on the aggregate distribution of field soils*

Mean moisture percentage on air-dry basis	Arable			Allotment		
	19	15	0	24	18	0
Percentage of soil on:						
1¼ in. sieve	19·5	29·5	16·0	5·5	19·0	19·5
⅝ in. sieve	25·5	30·5	32·0	14·0	11·0	15·0
¼ in. sieve	25·0	16·0	21·0	21·5	16·0	15·0
3 mm. sieve	24·5	15·5	20·0	35·0	27·5	24·5
Passing 3 mm. sieve	4·5	8·0	11·0	24·0	27·0	25·5

very poor in humus while the allotment soil, which was taken less than 200 yd. away from it, has been enriched with organic residues for the last seventy years. They were sampled after a wet spell in winter and sieved immediately, and although both soils were wet there was no

serious sieving trouble. Some samples were then partially dried and others completely air-dried and again sieved.

There is obviously a tendency for the proportion of the largest and of the smallest clods to increase as drying commences. The explanation may be either a secondary alteration of the initial soil structure due to the drying, or a more accurate representation of it due to the mechanical strengthening of the larger lumps so that they do not break down during sieving, and to a more efficient separation of the smaller lumps on the finer sieves since they no longer stick together. It is not possible to decide which of these alternatives is occurring, though the latter is probably the more important. If this is so, sieving the soil partially dry gives a better representation of the size distribution of the wet aggregates in the field than sieving it wet.

The effect of air drying seems to be erratic. It is possible that under these conditions it is worth following Volkov (1933) and using violent mechanical sieving, to give the distribution of mechanically strong aggregates, rather than attempt to determine the distribution of the wet aggregates in the field.

The second general method of determining the size distribution of wet aggregates is to sieve the soil in a liquid in which the wet crumbs neither stick together nor slake. An obvious liquid to try is benzene, for wet clods certainly do not slake in it, but unfortunately the finer crumbs stick together on the sieves almost as badly as if they were sieved in air. An attempt was made to overcome this difficulty by using an alcohol-benzene mixture, for wet crumbs do not stick together in alcohol, though they slake. It was possible that a suitable mixture could be found in which the crumbs did not slake, as in benzene, and did not stick together, as in alcohol. But it was found that the minimum concentration of alcohol needed to prevent sticking was sufficient to cause appreciable slaking, so that this method fails.

A good analysis can, however, be made if all the clods are smaller than about ¼ in. by putting the wet sample on a filter, washing out the water with acetone and then sieving gently in air. The method has no general validity as larger wet clods slake appreciably in acetone, and no improvement is obtained by using dioxan (diethylene dioxide) instead of acetone.

The conclusions are that it is possible to obtain without great difficulty figures for the size distribution of the aggregates in the field which will have considerable value provided the soil is not too wet. A reasonable estimate of the size distribution of wet aggregates can

probably be obtained by sieving soils with large clods after the sample has dried a little and for soils with small clods after it has been washed with acetone.

THE SIZE DISTRIBUTION OF WATER-STABLE AGGREGATES ON SOIL CRUMBS

The determination of the size distribution of the crumbs or water-stable aggregates in a soil is an attempt to measure some more fundamental property of the soil aggregates than is obtained by simple sieving of the field soil. The concept of water stability is vague, since it takes no account of such important factors as the method and the rate of wetting. Its justification is that it gives in practice quantitative information that is known to be qualitatively correct, which is unobtainable by simple sieving in air.

The methods in general use fall into three general categories: sieving under water, elutriation and allowing the soil crumbs to settle from a suspension and determining the size distribution either with a hydrometer or by some such device as introduced by Cole & Edlefsen (1935).

Tjulin's (1928) description of the sieving technique was the first generally available to non-Russian readers. This technique, the principle of which is to put some wet soil on top of a bank of sieves and sieve gently under water, is only suitable for, and is the only one suitable for, aggregates larger than about $\frac{1}{4}$ mm. Elutriation of the wet soil in a standard elutriator is only suitable for grading crumbs between about 0·5 and 0·02 mm. in size. Both these techniques subject the crumbs to mechanical shocks and abrasion, which though of quite minor importance in the elutriator, where all the crumbs are small, becomes of major importance in the sieving methods where the crumbs are very much larger.

The third method consists in dispersing the soil crumbs uniformly throughout a column of water and then determining the weight concentration at a given height at successive time intervals (hydrometer) or at successive heights after a given time interval (Cole-Edlefsen tube). This method is only suitable for crumbs smaller than 0·07 mm. if the hydrometer, and 0·15 mm. if the Cole-Edlefsen tube is used. During the analysis the crumbs are of course subjected to no mechanical shocks, so that these methods should give a better estimate of the size distribution of the water-stable crumbs than the sieve or elutriator methods, but this advantage is largely offset by the difficulty of dispersing the crumbs

uniformly throughout the settling column without disintegrating them in the process.

The sieving technique

Two main methods of sieving are in general use, namely manual and mechanical sieving. Only manual sieving will be discussed here for reasons that will be given later in this section. The actual experimental procedure employed at Rothamsted is as follows: Brass sieves, 15 cm. in diameter, are used, and the bank is usually made up of six sieves suitably chosen from the following eight: 7, 4, 3, 2, 1, ½ mm. and the 100 and 200 mesh. Thick rubber bands, cut from old inner tubes of motor-car tyres, are placed round the junction of one sieve with another to keep the contents of the lower sieve from escaping when the bank is being immersed. The sieving is done in large glass accumulator jars filled with ordinary tap water to such a level that when the bank is standing on the bottom the water comes half-way up the top sieve. The wet soil is put on the top sieve when it is thus half filled with water, and the bank then pulled up out of the water and left out till all the water has drained out of the first few sieves and then is plunged in the tank until the water has risen through the top sieve again. The efficiency of this sieving can be greatly increased by skilful manipulation of the sieves as they are being pushed down into the water and when they are just submerged, for by suitably twisting and tilting the sieves it is possible to ensure that all the crumbs move across the sieve slowly and so have a chance of falling through.

Another fundamental point in the technique of sieving is the number of times the sieves should be dipped in the water. The mere act of sieving breaks up aggregates, as is shown in the following example. A soil passing the 100 mesh sieve was well-mixed with a suitable quantity of water, frozen and thawed. A sample was then placed on top of a bank of sieves which were dipped in water 20 times. On examination it appeared that only well-formed crumbs were present on each sieve and that the sieving had been efficient. The sieves used were 7. 4, 3, 2, 1 mm. The 4 mm. sieve was then taken and another set of 3, 2, 1 mm. sieves put underneath and the whole dipped 20 times. A new set of sieves was then put under the 4 mm. and the whole dipped 40 times in another tank, and this was repeated with another set of sieves and dipped 80 times. The original 3 mm. crumb fraction was then treated in the same way, and then the 2 mm. and the 1 mm. also. The results for the different fractions were similar, and those for the 4 mm. fraction are given in Table III as an example.

Table III. *The effect of repeated sieving on crumb break-up*

	4 mm. crumbs			Total dippings	Percentage of initial weight
Initial weight in g.	16·0	12·0	7·9		
No. of times dipped	20	40	80	140	—
Weight on 3 mm. sieve	2·7	2·2	2·2	7·1	44
2 mm. sieve	0·3	0·2	0·3	0·8	5
1 mm. sieve	0·2	0·1	0·1	0·4	3
Passing 1 mm. sieve	0·8	1·6	1·5	3·9	24
Total break-up	4·0	4·1	4·1	12·2	76

It can be seen that 76% of the initial 4 mm. crumb fraction passed through the 4 mm. sieve during these 140 dippings, but 44% stayed on the 3 mm. and 24% passed the 1 mm. sieve. This behaviour is typical of all the experiments performed, namely that repeated sieving leads to a small reduction in the size of the crumbs and to a quantity of much finer aggregates.

The results of these experiments are not in accord with those of Pigulevsky (1936). He found that the absolute weight of soil passing through a sieve per dipping after a certain number of dippings became constant, and he therefore corrects his final weight by adding to it his estimate of the break-up. This correction cannot be applied here as his linear relation between the weight of soil on the sieve and the number of dippings does not hold.

The problem is even more complicated with fine wire-woven sieves such as the 100 and the 200 mesh sieves, as these sieves, particularly when not absolutely new, are not 100% efficient, that is, there are some apertures that are wider than the standard size.

This becomes a serious source of error if long-continued sieving is necessary, for if one sieves long enough the effective aperture of the sieve is that of its widest. Keen & Haines (1923) examined the magnitude of this error and showed that an appreciable proportion of the apertures of used sieves enclose areas 75% larger than the standard. This inefficiency of normal sieves in good, though not brand-new condition, is shown in the following example. Three ignited sand fractions $\frac{1}{2}$ mm.–100 mesh, 100–200 mesh and passing 200 mesh, were prepared as carefully as possible. Ten g. samples of each were taken and the mixture was then sieved under water. The results of a typical experiment are given in Table IV.

The main part of the separation is finished after 5 dippings on the 100 mesh and after 15 on the 200 mesh sieve, and most of the subsequent loss must be due to the irregularities of the sieve apertures, and possibly

to the sand particles not being spherical, so that they can pass through the apertures in some orientations and not in others. This latter trouble is naturally inherent in all sieving technique, as it will take irregularly shaped particles a long time to get into the orientation in which they can pass through the minimum-sized circular or square hole.

Table IV. *Effect of repeated dippings of fine mesh sieves containing sand*

	Weight of sand in g. on	
	100 mesh sieve	200 mesh sieve
Initially	30	10·9
After 5 dippings	10·4	9·3
15 dippings	9·9	7·7
35 dippings	9·4	7·0
55 dippings	9·0	6·0
Weight should be	10·0	About 9*

* The design of the experiment precluded any accurate determination of this quantity.

The sieving technique in use at the present time is to sieve the soil on the full bank 5–10 times, allowing the soil crumbs to move gently over the surface of the sieve. No exact number of dippings is used, as it appears better to judge by eye when the sieving is reasonably complete. The top sieve is then removed and the remainder of the bank sieved about another 5 times, the sieve removed and the process repeated until the last sieve has been done. The technique is somewhat unfair to the finer fractions, as they are subjected to more dippings than the coarser, but it has the merit of being the gentlest technique so far employed. If the size distribution of mechanically stronger water-stable crumbs is wanted, a more vigorous sieving technique, such as that of Pigulevsky (1936) or Yoder (1936), can easily be employed, but the authors prefer to keep the actual break-up of the crumbs on the sieves as low as possible and to vary the wetting conditions.

The elutriator technique

The elutriators used were of the Kopecky type, and each had four cylinders which were suitable for collecting particles with equivalent diameters larger than 0·2 mm., 0·1 mm., 0·05 mm. and 0·02 mm., and the particles passing through an elutriator were collected on a large Büchner funnel attached to a filter pump. This has the advantage that all the crumb fractions can be determined directly and are available for further examination if necessary. The technique used is not entirely satisfactory since in general if 20 g. of soil are elutriated, the sum

of the crumb fractions collected is about 19 g. The reason for this 5% loss has not been found; some material may pass through the filter papers on the Büchner funnel, and losses may also occur during the manipulation of the elutriation cylinders.

The elutriator separates out particles with different settling velocities, and equivalent particle sizes can only be obtained by using Stokes' Law. But it is subject to two sources of error. The minimum settling velocity of the particles in a cylinder is calculated on the assumption that the water flows at a constant velocity which is equal at all points across a certain cross-section of the cylinder normal to the direction of flow. This condition is not in fact fulfilled in any elutriator since, particularly in the larger cylinders, there is a definite flow of water down the inner walls of the cylinders. This effect does not diminish the sharpness of the separation of settling velocities, but it does affect, to an unknown extent, the actual value at which this separation occurs.

There is a second source of error which affects the sharpness of separation without affecting the settling velocity limits of the cylinders. Small bubbles of air attach themselves to crumbs, causing them to be carried either into a larger cylinder than corresponds to their settling velocity or right out of the elutriator. These bubbles may come from the crumb itself, in which case the method of wetting the soil was inefficient, or from the water, when all one can do is to keep the elutriator going for as short a time as possible.

Two points of technique have been investigated, namely the minimum time necessary for a good separation and the maximum weight of soil that could be used. Three hours was found to be a sufficient time for elutriation, and duplicate determinations usually agreed to within 5% if 20 g. of soil were used. Two hours was too short a time and duplicate determinations often varied by more than 20%. No effect of load was found even with 8 g. of soil in each of the last three cylinders. Four fractions were carefully prepared, which had settling velocities belonging to the second, third and fourth cylinders and to that fraction passing through the elutriator. Composite samples were prepared by mixing either 2 g. of each fraction or 4 g. or 8 g., and these composite samples, weighing either 8, 16 or 32 g., were then elutriated for 3 hr. An example of the results is given in Table V, which shows that any effect of load is more than swamped by the random errors of elutriation.

The conclusions reached about the elutriator technique during this work is that it is a very satisfactory method of grading soil aggregates finer than about ½ mm. in size, and is the only one in common use which

collects sub-fractions so that they can be examined in more detail by other methods. Its minor disadvantages are that elutriators are large, rather costly and need a stream of water, but its main objection is that one elutriator can only perform two separations per day, so that if many separations must be made, a battery of elutriators is required and these take up a considerable area of laboratory bench space.

Table V. *The effect of load on the efficiency of elutriation*

	Percentage of sample in each fraction after 3 hr. elutriation		
Mean weight of sample per cylinder in g.	2	4	8
Cylinder 2, 0·2 –0·1 mm.	27	23	28
3, 0·1 –0·05 mm.	23	22	23
4, 0·05–0·02 mm.	28	30	30
Passing out <0·02 mm.	22	25	19

The hydrometer technique

The hydrometer has only limited possibilities for aggregate analysis, for it can barely be used for particles larger than 0·07 mm., i.e. with settling velocities larger than 0·3 cm./sec. Its advantages are its cheapness, speed and simplicity, and its disadvantage its inherent inaccuracy.

The hydrometer used in these experiments had a bulb about 8 cm. long and 1·8 cm. diameter and a scale nearly 10 cm. long with a hundred graduations between 1·000 and 1·100. The experimental technique used was to disperse wetted soil gently and uniformly in a measuring cylinder containing a given volume of suspension, then the hydrometer was put in and readings taken after successive time intervals. The results of typical experiments made in this manner are given in Table VI, which shows that the apparent size distribution of a sample does depend on the actual concentration of the soil suspension in the settling cylinder. The figures given in the table were obtained by taking a series of hydro-meter readings in suspensions of four different concentrations at successive intervals of time, dividing the readings in the 5, $7\frac{1}{2}$ and 10% suspensions by two, three and four respectively to make them comparable to the readings in the $2\frac{1}{2}$% suspension, plotting these on a settling velocity-hydrometer reading graph, and reading off the smoothed hydrometer reading at arbitrary settling velocities. This procedure is necessary as the actual settling velocity for a given time depends on the hydrometer reading, as the lower the reading the deeper the bulb is in the liquid and the greater is the limiting particle settling velocity at that time.

Table VI. *Effect of soil concentration on hydrometer readings*

Hydrometer readings in 0·001 units of density reduced to $2\frac{1}{2}\%$ soil concentration

Soil conc. in % ...	$2\frac{1}{2}$	5	$7\frac{1}{2}$	10
Settling velocity cm./sec.				
0·3	5·0	6·6	6·9	7·9
0·2	3·7	6·0	6·2	7·1
0·15	3·0	5·1	5·6	6·3
0·125	2·2	4·4	5·1	5·9
0·1	1·2	3·5	4·5	5·1
0·075	0·0	2·4	3·5	4·3
0·05	0·0	1·1	2·3	2·9
		0·0	0·4	0·8

The results of other experiments have been similar. Expressed on the $2\frac{1}{2}\%$ concentration basis, the mean difference between the $2\frac{1}{2}$ and 5% suspension is just over 2 units, and between the 5 and 10% suspension about $1\frac{1}{2}$ units when the hydrometer is giving an appreciable reading. This difference could be due to three causes:

1. The failure of Stokes' Law. If this is the cause the $2\frac{1}{2}\%$ suspension probably gives the most accurate result, for presumably the more concentrated the suspension the slower the particles settle.

2. Soil settling on top of the hydrometer bulb, pressing it down and so making it give too low a reading. It is not possible to predict how this will depend on the concentration of the suspension, but if the weight of soil on top of the bulb is nearly independent of the concentration, this disturbing effect will be smaller for the more concentrated than the less concentrated suspension.

3. Disturbances in the rate of sedimentation of the particles in the soil suspension due to mass movements of the suspension in the settling column. Several agencies cause these mass movements, such as the motion of the hydrometer bulb floating in the suspension and the lowering of the density of the suspension just under the hydrometer bulb due to the bulb preventing soil particles from reaching this region from above. It is not known if the errors due to these causes are proportionately greater or less in dilute than in concentrated soil suspensions.

One further point of hydrometer technique is that the cylinder containing the soil suspension must have an adequate diameter. The diameter of the cylindrical bulb of the hydrometer used in these experiments was 1·8 cm., and if it was used in a cylinder of diameter 4 cm., it gave readings that on the $2\frac{1}{2}\%$ concentration basis were about 0·3 of a unit lower than in cylinders of diameter 5 or 6 cm.

There is an alternative technique available which uses the hydrometer

to determine the density of the suspension at the end of a definite time interval. The soil suspension is allowed to sediment for a given time and the hydrometer is then put in. This method suffers from the same defect as the first technique for very short settling times, which is just the region where it would be most useful for aggregate analysis. Investigations are in progress to discover how far these difficulties limit the use of the hydrometer for mechanical analysis.

The hydrometer technique, although very simple, is thus only suitable for giving approximate results for soils whose aggregates are less than 0·07- 0·05 mm. when separated fractions are not needed for further analysis.

The Cole-Edlefsen tube

The principle of the method is very similar to that of the hydrometer method, but whereas in the hydrometer method the size distribution of the soil particles is determined from the variation with time of the density of the soil suspension at a given depth, in the Cole-Edlefsen tube it is determined directly from the weight of particles present at different depths of the settling column after a given settling time, usually $\frac{1}{2}$, 1 or 2 min.

Cole & Edlefsen (1935) use a brass tube 30 in. long, closed at each end with aluminium caps, inside which fits another tube cut into fifteen 2 in. sections. The tube is almost filled with water, a known weight of soil is put in, and the tube then completely filled and closed. The soil is uniformly dispersed throughout the tube by repeatedly inverting the tube after suitable intervals of time. The tube is then stood vertically upright for the soil particles to settle for the requisite time and it is then left horizontal for a number of hours to allow all the soil that was in each section to settle on to the side of the section. The water is then allowed to run out of the tube slowly and the weight of soil on each section determined.

This method, like the hydrometer, subjects the aggregates to the absolute minimum of abrasion during settling. It has certain minor advantages over the hydrometer in that it is in many ways more accurate and can be used for settling velocities up to 1·5 cm./sec. (equivalent diameter 0·13 mm.) instead of only 0·3 cm./sec. Unlike the hydrometer method, however, it is neither a rapid nor a simple determination to make.

The efficiency of the method is limited by the accuracy with which it is possible to disperse the soil crumbs and particles uniformly throughout the suspension before sedimentation begins. At first, following the

technique suggested by Cole & Edlefsen, very poor uniformity was obtained but this was improved considerably by altering the time intervals between successive inversions of the cylinder. In spite of this, however, the lack of agreement between duplicate determinations has in fact been so poor that the results were no more accurate than those obtained by the hydrometer.

The comparison of the methods

Any direct comparison of sieving with the other methods is artificial since its optimum range is so much higher. For soils in good structure, as for example many heavy meadow and woodland soils, in which 60% of the water-stable crumbs may be larger than $\frac{1}{4}$ mm., sieving is the only method available.

Hence unfortunately the sieving technique must be used for very many interesting soil types in spite of the fact that the ability of an irregularly-shaped crumb to pass through a sieve opening is a vaguely defined concept and that the mere act of sieving water-stable crumbs may break an appreciable proportion of them up into smaller crumbs.

If the majority of the water-stable crumbs are smaller than say 0·1 mm., the hydrometer method will normally be perfectly adequate provided separated crumb fractions are not required, while if they are, elutriation is essential.

On sampling for Tjulin sieve analysis

In normal practice it is not advisable to sieve soil samples of more than 50–100 g. under water if sieves of 15 cm. diameter are used. But some soils may contain clods weighing several hundred grams each, so that it is obviously impossible to take a 100 g. sample representative of the clod structure of these soils. It is now standard practice at Rothamsted to sieve the air-dry sample on a $\frac{5}{8}$ in. sieve before analysis, analysing separately the fraction passing and that retained by the sieve.

Using a soil sample that has passed the $\frac{5}{8}$ in. sieve only reduces, without removing, the difficulty of taking a 100 g. sub-sample having the same clod size distribution as the main sample. A typical example of the magnitude of this sampling error is given in Table VII. Eight 100 g. samples were taken as carefully as possible from a 2 kg. sample of air-dry soil that had passed the $\frac{5}{8}$ in. sieve. These sub-samples and the remainder of the sample were then each sieved separately. In the table the clod distribution for the whole sample before analysis, computed

from the sum of all these separate sievings, is given, as well as the mean
clod distribution for the eight sub-samples and the largest deviation of
any sub-sample above and below the mean.

Table VII. *Variability of clod analysis of sub-samples
from an air-dry bulk sample*

Percentage of soil

	Whole soil	Mean of eight 100 g. sub-samples	Largest deviation from mean	
			Positive	Negative
On ¼ in. sieve	31·0	29·3	11·5	3·9
3 mm. sieve	33·2	31·8	4·3	5·9
1 mm. sieve	25·0	27·2	2·9	5·4
Passing 1 mm. sieve	10·8	11·6	4·5	3·4

This table shows that variations of about 5 % in the clod size distri-
bution above and below the mean are usual, and this is typical of the
order of variability found in all the other experiments carried out here.

Several experiments have been made to determine the effect of this
variability in the clod distribution of the sub-samples on the variability
in their water-stable crumb distribution. Table VIII gives the results of
one of these experiments. Four 100 g. sub-samples taken as above were
sieved under water and the results were compared with those for four
100 g. composite samples made by mixing together the different sized
clods in the proportions in which they were present in the main sample.
The table gives the mean crumb distribution and the range of the
individual determinations for these two sets of samples, the range of a
set of determinations being the difference between the highest and the
lowest value. The variability of the crumb analysis of these two types

Table VIII. *Variability of the crumb analysis of sub-samples
taken in different ways*

Soil: Knott Wood, passing ⅝ in. sieve

Crumb fraction	Sub-sample taken direct		Composite sub-sample		Ratio of range	Mean ratio 4 soils
	Mean	Range	Mean	Range		
>3 mm.	27·0	17·1	27·8	16·6	0·97	0·71
3–2 mm.	9·0	3·4	8·2	5·4	1·59	1·17
2–1 mm.	15·7	3·7	16·3	3·2	0·97	1·11
1–½ mm.	14·5	4·0	13·5	5·2	1·30	0·81
½ mm.–100 mesh	12·9	6·3	13·0	8·7	1·38	1·01
100–200 mesh	4·2	2·0	4·6	2·4	1·20	0·99
Passing 200 mesh	16·7	9·5	16·6	7·3	0·78	0·89
					Mean	0·96

of samples is compared by use of the ratio of their ranges. If the ratio is less than unity the composite samples give more uniform results and if greater than unity less uniform results than the sub-samples directly. The last column of the table gives the mean value of the ratio of these ranges for the four soils examined at this time.

The table shows quite clearly that in spite of the variations in the clod analysis of the sub-samples taken direct, their crumb analyses were no more variable than composite samples made up with identical clod analyses.

This result is not in accord with those of Savvinov (1931) and Tsyganov (1935), who found that the composite samples gave a definitely lower variability than the natural soil. But this lack of accord is more apparent than real as the soils used in our experiments were previously sieved through a $\frac{5}{8}$ in. sieve. Two troubles arise when clods larger than $\frac{5}{8}$ in. are used, firstly, there is the difficulty of ensuring uniform slaking and secondly, only a very few clods can be analysed at one time owing to their weight. A number of comparisons have been made between the crumb-size distribution of the clods passing a $1\frac{1}{2}$ in. but retained on a $\frac{5}{8}$ in. sieve and of the soil passing the $\frac{5}{8}$ in. sieve. The means of several comparisons of three different soil types are given in Table IX.

Table IX. *Crumb analysis of the clods between* $1\frac{1}{2}$ *in. and* $\frac{5}{8}$ *in. in size and of the residual soil passing a* $\frac{5}{8}$ *in. sieve*

	Old arable		New pasture 15 years old		Old woodland	
Crumb fraction	Clods	Soil	Clods	Soil	Clods	Soil
>7 mm.	0·0	0·0	6·1	—	30·9	—
3 mm.	0·0	0·0	5·9	5·7	9·5	27·2
2 mm.	2·7	0·2	5·2	4·5	5·0	9·4
1 mm.	3·8	4·9	16·7	15·6	12·5	16·6
$\frac{1}{4}$ mm.	18·0	13·3	19·9	22·4	9·9	13·9
100 mesh	35·0	42·6	18·9	24·8	12·0	14·3
<100 mesh	40·6	39·0	27·2	27·0	20·2	18·6

On the whole, the clods and the residual soil give similar crumb distributions, though there is a tendency for the clods to give a higher proportion of the larger crumbs than the soil, probably due to the slower rate of wetting of their interiors.

The conclusion arrived at from these experiments is that if the soil is lumpy, it is worth while carrying out the crumb analysis in two parts, on the soil retained by a sieve with aperture between about $\frac{3}{4}$–$\frac{1}{2}$ in. and on the soil passing this sieve. The crumb analysis for the soil as a whole would be calculated by combining these two analyses in their

correct proportion. This is probably unnecessary for many arable soils but is of great importance for pasture soils, for otherwise the deviations between duplicate determinations of the crumb distribution may be so large as to make the analyses worthless.

THE PRE-TREATMENT OF THE SOIL SAMPLE FOR CRUMB ANALYSIS

There are two points of pre-treatment that must be settled before the crumb analysis can commence, namely the moisture content of the sample and the method by which it is wetted.

There are two obvious soil moisture contents to choose between the field-moisture content at the time of sampling and the air-dry state. If the field-moist condition is used, the sample should be analysed as soon as it is brought to the laboratory, and not left for several days in a sealed container, as the microbiological activity taking place in the sample may alter the crumb stability. If the soil is air-dried first, it can be left for a considerable time before analysis. Hence if a large number of samples have to be taken on the same day, the use of the air-dry soil is almost obligatory.

The method of wetting the soil affects the water stability very markedly. The more rapidly a soil is wetted the lower is the crumb stability, provided the wetting does not take place *in vacuo*. Table X gives three examples of the effect of different methods of wetting a soil which is itself at different moisture contents.

The details of the wetting techniques used were as follows. In all the methods the soil to be wetted was put on a filter paper on the bottom of a sieve standing in a large glass dish. For wetting by immersion sufficient water was poured into the dish, but not on to the sieve, to immerse the soil sample completely. For wetting by capillarity, just enough water was added to wet the filter paper. In both cases the arable soils were left for 30 min. and the woodland soil for 2 hr. before sieving. Wetting by fine spray was done by repeatedly spraying on water from a fine scent spray until the sample appeared to be saturated and then leaving it for 2 hr. before sieving. For wetting under vacuum a high quality vacuum desiccator is essential. Great care over two points must be taken if the effect of the soil air is to be reduced to negligible proportions. Firstly, a much better vacuum than is obtained by a filter pump is needed, and in fact a Hyvac oil pump was used which reduced the gas pressure over the soil to less than 1 mm. Secondly, pumping does not seem to remove all the air from many soils and for a smooth

and gentle wetting of these a slow stream of air-free water vapour must be passed over the soil for about an hour. Air-free water is then run into the desiccator until the water level just covers the filter paper· The soil is then left for 30 min. for the arable and 2 hr. for the woodland soil. Air is then let into the desiccator and the soil sieved.

Table X. *Effect of the method of wetting and the moisture*
content of the soil on its crumb stability

Percentage of water-stable crumbs larger than 1 mm.
Arable soil: Broadbalk

	Heavily dunged. Plot 2			Starved. Plot 3		
	Field moist	Air-dry	Oven-dry	Field moist	Air-dry	Oven-dry
Moisture content	23·6	2·4	0·0	17·3	1·7	0·0
Method of wetting:						
Under vacuum	74	77	84	65	71	78
By capillarity	64	9	16	54	5	7
By immersion	63	4	7	36	2	3

Woodland soil: Knott Wood

	Air-dry	Oven-dry	Dried over P_2O_5 *in vacuo*
Moisture content	2·49	0·04	0·00
Under vacuum	66	66	79
By fine spray	68	63	63
By capillarity	50	60	68
By immersion	41	59	53

The table shows that drying a soil from its field-moist to its air-dry condition reduces the crumb stability unless the disturbing effect of the entrapped or adsorbed air is eliminated by using the vacuum wetting technique, when drying slightly increases it.

The problem of choosing what method of wetting and what soil moisture content to use thus depends on what information is required. There is no intrinsically best choice. If the stability of the dry-soil structure to gentle rain is required obviously one would wet the air-dry sample by capillarity or a fine spray, while if its stability to flood irrigation is wanted wetting by immersion is preferable. For many purposes there is much to be said for doing two or three separate determinations of crumb stability using different methods of wetting. Pigulevsky (1936) suggests that the crumb stability should be determined on the air-dry sample only, using a slow and a rapid rate of wetting. He used wetting by a fine spray and by immersion as his slow and his rapid rates, and called the crumbs so obtained conditionally and absolutely water stable respectively. He found that the size distribution of the absolutely water-stable crumbs was only a little finer than that

of the conditionally stable crumbs for meadow soils but very much finer for arable soils. The results given in Table X are obviously in accord with this, since the effect of the rate of wetting on the crumb-size distribution is only small for the woodland soil but very large for the arable.

A further method of pre-treatment, only relevant for the elutriator or hydrometer technique, has been introduced by Middleton (1930) and Demolon & Hénin (1932), which consists in dispersing the soil sample fairly vigorously in water before analysis, by shaking it for example in an end-over-end shaker for a definite time. This type of pre-treatment is well suited to determine the size distribution of the soil crumbs produced when a surface soil is subjected to the erosive action of a cloud burst, but it appears to have only very limited applicability to soils of the temperate regions. It does not determine the ultimate aggregates in a soil, for direct microscopical examination shows that often the aggregates so obtained are themselves clusters of still smaller aggregates.

THE SEPARATION OF CRUMBS FROM SAND IN A CRUMB FRACTION

1. *The direct method*

The preceding analysis of the distribution of water-stable crumbs in a soil actually gives no direct estimate of the quantity of such crumbs, for the crumb fractions which they give will in general contain both crumbs and unaggregated soil particles having the same range of sizes or settling velocities as the crumbs. Each crumb fraction should therefore be subjected to further analysis to determine the proportion of crumbs and sand it contains.

It has been found possible to separate out the crumbs from the unaggregated sand grains in the crumb fractions between 1 and 0·05 mm. in size. The method consists in dispersing the crumb fraction carefully in a mixture of carbon tetrachloride and bromoform and adjusting the density so that the unaggregated sand particles sink while the crumbs float. The separation is not very sharp, but with practice has given satisfactory results. There is always a certain loss of soil, but it is usually less than 5%. When the separated fractions were examined with a mineralogical microscope between crossed Nicols, the sand separate appeared to consist almost entirely of sand grains and the crumb separate of crumbs, though there were always a few sand grains visible in it.

Table XI gives an example of the efficiency of this separation of sand

grains from the crumbs, and it shows that the silt and clay content of the sand separate have been reduced to very small proportions.

Table XI. *Mechanical analysis of sand and crumb separates*

	Sand separate	Crumb separate	Whole fraction	Computed whole fraction
Sand	95·4	45·8	75·0	77·9
Silt	1·6	28·0	11·0	10·1
Clay	1·4	21·7	9·7	9·7

The last column of the table gives the mechanical analysis of the whole fraction computed from that of the sand and the crumb separates and their proportional weight.

Table XII gives a further illustration of the efficiency of the method where the base exchange capacities of the separates have been used instead of the mechanical analysis. The method of determining the base exchange capacity is described in the next section.

Table XII. *Base exchange capacity of sand and crumb separates*

Soil: Broadbalk

		Sand separate	Crumb separate	Whole fraction	Computed whole fraction
Plot 2.	1–½ mm.	1·9	25·0	19·5	21·9
	0·2–0·1 mm. (1)*	1·6	26·1	19·0	19·7
	(2)	1·6	27·5	13·0	11·3
	0·1–0·05 mm.	1·6	25·0	20·0	21·4
Plot 3.	0·2–0·1 mm. (1)*	1·6	19·1	12·5	12·5
	(2)	1·6	19·1	8·5	7·0
	0·1–0·05 mm.	1·6	17·5	13·7	15·0

* (1) and (2) refer to crumb fractions prepared by different methods of crumb analysis.

This method of separation is thus reasonably efficient for the particular type of soil that exists on the Rothamsted farm. But it is obviously not a routine method, as it is much too slow and expensive. It does, however, give a good separation for research purposes.

II. *Indirect methods*

Several methods have been devised to overcome the difficulty presented by carrying out an exact separation of the sand grains and the crumbs. One method that has been used is to assume that if the lower size limit of a crumb fraction is d, then all the sand particles larger than d in that fraction are unaggregated, an assumption which may be badly wrong for some soils.

A second type of method is to limit the definition of crumbs. Instead of determining the proportion of crumbs in the fraction, some more easily measurable property is chosen. Thus one can determine the amount of

clay, or of clay+silt or of exchange capacity in each crumb fraction and discuss this distribution instead of the crumb distribution. These methods have the advantage that they are measuring much more definite properties than the proportion of crumbs in a fraction, as it is impossible to give a useful exact definition of what shall be called a crumb and what a sand grain, or to decide how much clay and silt may stick on to the surface of a sand grain before it becomes a crumb.

There are certain theoretical reasons for choosing to measure the distribution of base exchange capacity rather than of clay content in the different fractions of most agricultural soils, for the base exchange capacity probably gives a more accurate measure of the amount of aggregating material in each crumb fraction of these soils than does the clay content. The clay-content figure naturally ignores the effect of organic matter, which certainly sometimes plays an important role in aggregation and, when the clay is defined as being smaller than 2μ, it may include many particles having only very little binding power. The base exchange capacity, on the other hand, fails to give useful information if the silt and sand particles possess any appreciable exchange capacity, as may happen on soils derived from basic igneous rocks, or if the clay and organic matter are very unequally distributed between the different crumb fractions, a condition that is probably rare.

The great advantage of choosing base exchange capacity is the ease and rapidity with which it can be determined. The method used here is due to Schofield (1933), and is based on the principle of determining the amount of base a soil holds when in equilibrium with a well-buffered solution of a suitable pH. The buffer solution used is an equi-molecular mixture of potassium carbonate and bicarbonate which is $0.15N$ in potash and has a pH of about 10. The soil is shaken with the potassium-carbonate solution, and all the exchangeable hydrogen, calcium and magnesium is replaced by potash and the equivalent amount of carbonate disappears from the solution. This method ignores all the exchangeable potash or soda in the soil but, since the proportion of these to the total exchangeable bases is presumably about the same in the different crumb fractions, this limitation is not serious. The actual experimental procedure used is to add a suitable quantity of soil to 25 c.c. of $N/5$ K_2CO_3 in a Pyrex boiling tube, shake slowly for several hours, allow to settle, pipette out 5 c.c. of the supernatant liquid and titrate with $N/20$ HCl using Bromo-Cresol-Green as the indicator. The amount of soil to be added should be such that about one-quarter of the carbonate has been removed.

Table XIII gives some examples of the use of this method for showing how the active material is distributed throughout the various crumb fractions obtained during the crumb analysis.

Table XIII. *Base exchange capacity of crumb fractions*

	Base exchange capacity in mg. equivalent per 100 g. fraction		
Crumb fraction	Woodland soil	Pasture soil	Arable soil
2–1 mm.	18·9	18·0	19·7
1–½ mm.	18·9	19·2	22·2
½ mm.–100 mesh	17·9	17·5	17·0
100–200 mesh	18·0	16·7	17·4
Passing 200 mesh	13·3	15·0	18·9

Table XIV gives an example of the distribution of exchange capacity throughout the crumb fractions of a garden soil, when the soil was sieved under water using 4, 2, 1, ½ mm. sieves and the material passing through was then run through an elutriator.

Table XIV. *Distribution of exchange capacity in crumb fractions*

Soil used: Allotment

Crumb fractions	Percentage of soil in fraction	Base exchange capacity (B.E.C.) of fraction	Contribution to B.E.C. of soil		Summation percentage	
			Actual	Percentage	B.E.C.	Crumb fraction
On sieves:						
>4 mm.	2·8	17·0	0·47	2·1	2·1	2·8
4–2 mm.	4·5	17·1	0·77	3·5	5·6	7·3
2–1 mm.	8·4	21·2	1·78	8·1	13·7	15·7
1–½ mm.	13·7	23·2	3·18	14·5	28·2	29·4
In elutriator:						
½–0·2 mm.	7·7	14·0	1·08	4·9	33·1	37·1
0·2 –0·1 mm.	23·0	24·2	5·57	25·4	58·5	60·1
0·1 –0·05 mm.	15·6	23·0	3·58	16·4	74·9	75·7
0·05–0·02 mm.	14·9	20·5	3·06	14·1	89·0	90·6
Passing 0·02 mm.	8·9	30·5	2·40	11·0	100·0	99·5
		Sum	21·89			

The computed base exchange capacity of the soil, found from the percentage of each crumb fraction and their base exchange capacities is 21·89, and the value determined direct was 21·7, giving excellent agreement. This is better agreement than is usually obtained, but the calculated and directly determined values for the base exchange capacity of the soil are usually well within one milli-equivalent.

The quantity of crumbs in each crumb fraction can be replaced by the quantity of clay in it instead of by its base exchange capacity. An example of this procedure is given in Table XV where the mechanical

analysis and the base exchange capacity of the various crumb fractions have been given.

Table XV. *Comparison of the mechanical analysis and the base exchange capacity of crumb fractions*

Soil: Barnfield Headland

Fraction	Sand	Silt	Clay	Base exchange capacity (B.E.C.)	Clay / B.E.C.	Silt / Clay
1 –0·5 mm.	53·8	21·9	24·3	17·7	1·37	0·90
0·5 –0·2 mm.	69·8	14·2	16·0	11·4	1·40	0·89
0·2 –0·1 mm.	56·0	22·4	21·7	16·6	1·30	1·03
0·1 –0·05 mm.	60·0	18·4	21·8	15·8	1·38	0·84
0·05–0·02 mm.	66·1	16·4	17·6	12·5	1·41	0·93
<0·02 mm.	1·7	53·1	45·2	28·2	1·60	1·17
Whole soil	50·0	23·7	26·4	17·7	1·49	0·90

The table shows that the clay content of the crumb fractions follows their base exchange capacity fairly closely with the exception of the finest fraction (< 0·02 mm.), which has more clay than would be expected from its base exchange capacity. This is a general result for all the Rothamsted soils so far examined, and may be connected with the fact that the ratio of silt to clay is always higher in this fraction than in the others. The mean results for five different determinations on three different soils are given in the following table. The ratios for the various soils have been reduced to a comparable basis by putting the ratios for the whole soils equal to 100, and taking the means on this basis.

Crumb fraction	Clay / B.E.C.	Silt / Clay
0·2 –0·1 mm.	93	103
0·1 –0·05 mm.	95	86
0·05–0·02 mm.	90	99
<0·02 mm.	117	125
Whole soil	100	100

For all the samples the two ratios for the fraction finer than 0·02 mm. were higher than for the other fractions and the silt/clay ratio was always lowest for the fraction 0·1–0·05 mm. Otherwise there were no consistent differences between the fractions.

Another point of general validity is brought out in Tables XIV and XV. The fraction between 0·05 and 0·02 mm. has always been found to have a lower base exchange capacity than the two fractions immediately larger, namely the 0·2–0·1 and the 0·1–0·05 mm. From the few complete determinations available this appears to be due mainly to the accumulation of fine sand in this fraction.

THE DEGREE OF AGGREGATION OR THE CRUMBINESS OF A SOIL

It is often desirable, particularly for routine determinations, to replace the crumb-size distribution curve of a soil by a single figure. But before this can be done the difficulty discussed in the previous section of distinguishing between the crumbs and the unaggregated·sand particles in a crumb fraction must be overcome and a suitable definition of the degree of aggregation must be decided upon.

There is no agreed definition of the degree of aggregation of a soil, nor does it yet seem desirable for there to be one. It is usually defined as the proportion of the soil, or of some soil component that is in crumbs larger than a certain size d. There is no *a priori* optimum choice for the crumb size d.

There is no theoretical minimum value since two clay particles aggregated together could be considered as a crumb, though this would be much too small to have any practical significance. There is, in fact, no single best choice of d suitable for all occasions, but a value lying in the range 0·5–0·1 mm. has much to commend it. The value of $d = 0·5$ mm. has usually been chosen at Rothamsted as giving the most informative figure for the degree of aggregation of the different soils studied.

Pigulevsky (1936) gave what appears to be an objective method for choosing the most appropriate value of d for any particular soil. He divides his crumb-fraction distribution curve into two parts, all fractions larger than a certain size being called positive fractions and all smaller negative. A crumb fraction is described as negative if a wet layer of it, 1 cm. deep, cracks on drying under standard conditions into newly formed clods which have an appreciable resistance to crushing. Pigulevsky states that for most soils the division between positive and negative fractions occurs fairly sharply between $\frac{1}{2}$ and $\frac{1}{4}$ mm. size. If this division is really found to be sharply defined, the proportion of all positive fractions instead of all fractions larger than some arbitrarily fixed size should obviously be used for specifying the degree of aggregation of the soil.

The actual weight of crumbs in the crumb fractions larger than d is not a convenient quantity to determine for routine purposes. A number of other quantities have been used instead, the two most common being either the percentage of soil particles smaller than d, or the percentage of clay or silt + clay, that are in the crumb fractions larger than d. One that is in general use at Rothamsted for control purposes is the proportion of the base exchange capacity of the soil that is in the crumb fractions

larger than d. For many soils, as for example that used for Table XIV, the proportion of the soil and the proportion of its exchange capacity that are in the crumb fractions larger than $\frac{1}{2}$ mm. are almost equal, being 29·4 and 28·2% respectively, but for some soils the difference can be considerable, and for this reason among others the base exchange capacity of each fraction is usually measured. Very often, however, the base exchange capacity of the 3 and the 4 mm. crumb fractions are not determined. In this case these crumb fractions are washed on a 1 mm. sieve and the stones retained on it weighed. This weight is then subtracted from the gross weight of the crumb fractions to give the nett weight of soil in them. The base exchange capacity of this soil is assumed to be that of the whole soil passing the 2 mm. sieve. This assumption usually introduces no appreciable error, as the nett weights of these crumb fractions are usually small.

SUMMARY OF THE CONCLUSIONS

1. It is possible to determine the size distribution of clods in the field by simple sieving of the soil without any pre-treatment provided the soil is not too wet. There is a personal factor involved in the sieving, but with care and training this will not affect comparisons of results obtained by that person. If the soil is too wet the individual clods smaller than 3 mm. stick together on the 3 mm. sieve. This sticking together is first apparent on the 3 mm. sieve but may become appreciable on the $\frac{1}{4}$ in. (6 mm.) sieve. No certain way was found for overcoming this difficulty.

2. There appears to be no best method for determining the size distribution of the soil crumbs, i.e. of the water-stable aggregates in the soil. The method and the technique must be chosen so as to give the maximum amount of useful information. If an appreciable proportion of the crumbs are larger than $\frac{1}{2}$ mm., a water-sieving method is practically essential.

3. The method of wetting to be used can only be chosen from a consideration of what information is wanted. If possible it would be desirable for general purposes to use a very slow or a vacuum wetting technique and a very rapid wetting technique such as wetting the soil by immersion in water.

4. The decision whether air-dry or field-moist soil should be used depends entirely on the information needed. For general purposes the use of air-dry soil is recommended.

5. Very lumpy soils must be sieved before it is possible to take a 100 g. sample. Pre-sieving the soil on a $\frac{3}{8}$ in. sieve appears to allow of good sampling. The distribution curves for the clods and the residual soil should be determined separately and that for the whole soil calculated from them.

6. It has been found possible to separate the crumb fractions of Rothamsted soil into crumbs and sand particles by carefully dispersing them in a bromoform solution of the correct density. The crumbs float and the sand particles sink.

7. A rapid method of overcoming this difficulty of distinguishing between crumbs and sand particles in a crumb fraction is to determine the proportion of the total base exchange capacity of the soil that is in each crumb fraction. Schofield's potassium carbonate method for doing this is described.

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REFERENCES

BOUYOUCOS, G. J. (1929). *Soil Sci.* **28**, 27–37.
COLE, R. C. & EDLEFSEN, N. E. (1935). *Soil Sci.* **40**, 473–9.
DEMOLON, A. & HÉNIN, S. (1932). *Soil Res.* **3**, 1–9.
KEEN, B. A. (1933). *Empire J. exp. Agric.* **1**, 97–102.
KEEN, B. A. & HAINES, W. B. (1923). *J. agric. Sci.* **13**, 467–82.
MANGELSDORFF, E. G. (1929). *Landw. Jahrb.* **69**, 485–519.
MIDDLETON, H. E. (1930). *U.S. Dept. Agric.* Tech. Bull. no. 178.
PIGULEVSKY, M. C. (1936). *Principles and Methods of the Experimental Study of Soil Deformations.* Selkhozgiz, Moscow, Leningrad.
PUCHNER, H. (1911). *Mitt. d. deutsch. landw. Gesellsch.* **26**, 38–40.
RUSSELL, E. W. (1938). Imp. Bur. Soil Sci., Harpenden. Tech. Comm. no. 37.
SAVVINOV, N. I. (1931). Quoted by TSYGANOV (1935).
SCHOFIELD, R. K. (1933). *J. agric. Sci.* **23**, 252–4.
TJULIN, A. F. (1928). *Perm Agric. exp. Sta. Division agric. Chem.* **2**, 77–122.
TSYGANOV, M. S. (1935). *Pedology*, 219–29.
VOLKOV, M. I. (1933). *Pedology*, 52–8.
YODER, R. E. (1936). *J. Amer. Soc. Agron.* **28**, 337–51.

EXPERIMENTS ON THE USE OF CHORIONIC GONADOTROPHIN (PREGNANCY URINE EXTRACT) FOR THE TREATMENT OF STERILITY IN DAIRY CATTLE

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THE magnitude of the annual loss to dairy farmers in this country due to bovine sterility is often not fully realized. Bartlett (private communication; see also Dairy Husbandry Department, National Institute for Research in Dairying, 1933), as a result of an extensive survey, finds that the average dairy cow generally leaves the herd at the peak of her productivity, and that of the various factors leading to disposal of dairy cows, sterility is the most important, approximately 25 % of all disposals being due to this cause. Disposals due to sterility are alone equal to the combined loss from recognized tuberculosis, contagious abortion and udder troubles. Hammond (1939) has summarized the various causes of sterility in cattle. In the first place, bulls may fail to produce sufficient spermatozoa and these may be of low vitality, conditions which may sometimes be cured by alterations of diet and management. Cows may fail to breed owing to infections of the reproductive tract, or by failing to come into oestrus, or they may be served regularly but nevertheless fail to become pregnant. In cases where sterility is due to ovarian cysts or to persistence of corpora lutea, treatment by manipulation, as advocated by Hammond (1939), usually gives satisfactory results. Sterility (other than that due to infection with *Brucella abortus* or *Trichomonas*), which cannot be treated by manipulation of the ovaries or by irrigation, may be due to endocrine disturbances, and might be expected to respond to hormone therapy. The use of such therapy, however, is at present in its infancy, and accordingly the following experiments on the treatment of certain forms of bovine sterility with pregnancy urine gonadotrophin are thought to be of some interest.

The cows used belonged to the herd of the University of Reading Farm which consists mainly of Dairy Shorthorns with some British Friesians. In addition, experiments were carried out on two cows belonging to this Institute. For the past four years there has been in the above herd a considerable amount of sterility which could be attributed neither to obvious deficiencies in nutrition or management nor to contagious abortion. In all cases only animals which were free from anatomical and pathological defects were experimented upon. All cases were subjected to veterinary examination before treatment, and had been pronounced normal and free from any obvious cause of sterility. No attempt was made to use cows with cystic ovaries, since it was considered that this abnormality is better treated in other ways. In addition, we had an opportunity of experimenting upon three sterile bulls, one of which belonged to the above herd. For access to the other two cases we are indebted to Mr N. P. Male, B.Sc., M.R.C.V.S.

Except where otherwise stated the human pregnancy urine extract used throughout this work was a specially concentrated preparation of Antuitrin "S" standardized at 500 rat units per c.c. (henceforward referred to as P.U.). For generous supplies of this material we are greatly indebted to Dr J. Stanley White of Messrs Parke Davis and Co.

RESULTS

Sterility in the bull

The three pedigree bulls discussed below had been referred for veterinary examination because, though once stockgetters, they had ceased to get cows in calf. Microscopic examination of the semen carried out by Mr N. P. Male revealed a deficiency in sperm number (actual counts were not done) together with absence of motility. It was thought probable that this condition might be due to hypofunction of the epididymis, which in turn might be due to failure of the interstitial tissue of the testes to secrete androgens. It has been found by Moore (1928) that in the ligated epididymis of the guinea pig, spermatozoa more rapidly lose their motility in the castrated than in the non-castrated animal. Further, injections of testicular hormone into castrates resulted in an increase in the period during which the spermatozoa retained their motility (Moore & McGee, 1928). If the above theory were true, pregnancy urine extract might be expected to produce beneficial results, since in rodents (Engle,

1929; Brouha & Simonnet, 1929) and monkeys (Engle, 1932; Aberle & Jenkins, 1934) pregnancy urine gonadotrophin stimulates the interstitial cells and thus indirectly the accessory organs.

Bull 1. This Dairy Shorthorn bull was 2 years 3 months old when treated. For some months he had failed to get cows in calf. Examination of his semen showed sperm of low motility. He was given two intramuscular injections of 2 c.c. P.U. on 6 May 1938 and 10 May 1938. Six days later his sperm were plentiful and fully motile. Up to the time of writing (about 18 months since treatment) he has proved entirely satisfactory as a stock-getter and has got 20 cows in calf, 28 services being required.

Bull 2. This was a 5-year-old Dairy Shorthorn bull. Some 3 years prior to treatment his semen was examined and was found to contain only a few immotile sperm. Subsequently he was turned out with heifers, some of which became pregnant. For 6 months prior to treatment no cows became pregnant by him. His semen was again examined and the findings resembled those of the previous examination. Two intramuscular injections of 2 c.c. P.U. were given on 24 March 1939 and 29 March 1939. Examination of his semen 43 days later showed a good number of highly motile sperm and he has since got cows in calf.

Bull 3. The semen of this 18-month-old Guernsey bull was examined because he was not stocking cows efficiently. It contained few motile sperms. His condition had not improved at a second examination 2 months later. In March 1939 two intramuscular injections of 2 c.c. P.U. were given with a 4-day interval. His semen was examined a week later and found to contain a large number of highly motile sperm. He has since proved satisfactory as a stockgetter.

The results of these three experiments indicate that chorionic gonadotrophin may be of great value in treating sterility in the bull, when endocrine deficiencies are suspected. It is fully realized that a larger series would have been desirable, but in our experience, clear-cut cases of this type appear fortunately to be rather rare. Nevertheless, these three experiments are of interest, since the practical value of such a treatment is obvious, especially where the bull concerned may be a valuable pedigree animal.

Sterility in cows

(a) *Failure to come into oestrus.* This condition is frequently associated with the presence of a cyst in the ovary or with the persistence of a corpus luteum. In such cases a cure can be effected by rupturing the cyst or squeezing out the corpus luteum. But even in the absence of the above conditions cows not uncommonly fail to exhibit oestrus. In such cases

sterility may be due either to a low rate of secretion of gonadotrophic factors by the pituitary, causing ovarian inactivity, or to a wrong balance of the follicle-stimulating and luteinizing hormones leading to a disturbance of the normal ovarian cycle. On the basis of experiments on other species (see Engle, 1939) it is reasonable to suppose that treatment with pregnancy urine extract might induce oestrus in a proportion of such cases, and indeed Zawadowsky, Eskin & Ovsjannikov (1935) found that injections of pregnancy urine extract caused ovulation and heat in cows.

Experiments were carried out on the administration of P.U. both by intravenous and intramuscular injection. In the case of intravenous experiments an injection of 3 c.c. was successful in one case and there were three cases in which 5 c.c. was followed by oestrus.

F. 20. This cow calved on 16 March 1938 and did not subsequently exhibit oestrus. She was given 3 c.c. P.U. intravenously on 19 May 1938 and came into season, and was served, on 20 May 1938. She was subsequently served on 18 June 1938 and again on 12 September 1938 and calved on 24 June 1939.

T.W. 8. Calved on 6 September 1937 and came into season on 14 November 1937 and not again. On 27 January 1938 she received 4 c.c. of commercial Antuitrin "S" (100 rat units per c.c.) intravenously without result. An intravenous injection of 8 c.c. of the same material on 3 February 1938 was ineffective. On 10 February 1938 she was given 5 c.c. of P.U. intravenously and came into season and was served on 11 February 1938. A further service on 23 March 1938 was necessary and she calved on 27 December 1938.

Bl. This cow belonged to the N.I.R.D. She calved on 15 November 1937 and did not subsequently come into season. She was given 5 c.c. P.U. intravenously on 11 May 1938 and came into season and was served on 12 May 1938 and then again on 10 October 1938. She held to the service on 10 October 1938 and calved on 24 July 1939.

F. 21. Maiden heifer which had been in oestrus many times. She came into season on 19 February 1938 and was given 5 c.c. P.U. intravenously on 28 March 1938. She was in season on 29 March 1938.

In addition to the above cases, there were two cases in which intravenous doses of 5 c.c. P.U. had no result by 13 days and 82 days after the last injection, and three cases in which doses of 3 c.c. intravenous had no effect by 20, 14 and 13 days respectively.

Among the cows given intramuscular injections there were two cases where oestrus followed three injections of 2 c.c. P.U. and one where a single injection of 2 c.c. was sufficient to induce oestrus.

T.W. 8. Had her fourth calf on 27 December 1938 and did not subsequently exhibit oestrus. She received intramuscular injections of 2 c.c. P.U. on 20, 22 and 24 February 1939 and came into season on 26 February 1939. She did not hold to this service but the next service on 2 March 1939 was successful. She calved on 12 December 1939.

C. 20. Calved on 14 July 1938 and did not subsequently exhibit oestrus. Her ovaries were examined on 13 October 1938 and reported to be flat. She was given four intramuscular injections of 2 c.c. P.U. on 13, 21, 24 and 26 October 1938. She came into season and was successfully served on 25 October 1938 and calved on 6 August 1939.

R 54. Did not come into season after calving. She received intramuscular injections of 2 c.c. Antuitrin on 21, 26 and 28 September 1938 and came into season on 23 September 1938. She was subsequently served again on 13 and 31 October 1938 and stood to the latter service, calving on 12 August 1939.

In addition there were four experiments in which four injections of 2 c.c. had no result by 10, 17, 19 and 50 days respectively, and three in which three injections of 2 c.c were negative for 10 days.

These experiments indicate that treatment with P.U. will cause oestrus in a proportion of cows which fail to come into season for reasons other than the presence of ovarian cysts or persistent corpora lutea. As far as can be seen from the limited number of animals used, intravenous administration is more likely to succeed than intramuscular, and 5 c.c. (2500 rat units) would appear to be necessary in most cases. It is necessary to record, however, that such high doses of this preparation may sometimes be dangerous to cows when given intravenously. A heifer which had never been seen in season was given four intramuscular injections each of 2 c.c. P.U. on 20, 22, 24 and 27 February 1939, without result. On 6 and 7 March 1939 she was injected by the Farm authorities with 5 c.c. of wheat germ oil. As she still did not come on heat she was given 5 c.c. P.U. intravenously on 10 March 1939 and she died later the same day. Post-mortem examination revealed no obvious cause of death, the only apparent abnormality being a slight enlargement of the heart Despite the fact that the protein content of P.U. is so small that it cannot be detected by ordinary reagents, it is possible that this death was due to anaphylactic shock. A second cow showed symptoms of distress after an intravenous injection of 2 cc. P.U. following shortly after 3 intramuscular injections, but soon recovered.

Probably, the failures to respond to P.U. injections were due to the lack of sufficiently ripe follicles in the ovary, and it is possible that in-

jections of pregnant mare's serum, which is rich in follicle-stimulating hormone, followed by luteinizing extract (P.U.) would have induced oestrus in these cases. On the other hand, the possibility that the cows had ovulated without showing any desire for mating (see Weber, 1911) must not be forgotten, particularly in view of the success of Day (1939) in mares and Zawadowsky *et al.* (1935) in cows, in inducing ovulation with chorionic gonadotrophin.

It should be noted that service at the heat induced by P.U. proved fertile in one case only (C. 20). In the other successful cases the injections served to re-activate the ovaries and pregnancy followed subsequent services. In this connexion it may be noted that Zawadowsky *et al.* (1935) found that services at heats induced by pregnancy urine extract were sterile.

(*b*) *Cows showing regular oestrus but failing to conceive.* Hammond (1939) considers that this condition is often due to an excess of luteal tissue in the ovary, which in turn causes the cervix to remain closed during oestrus and the mucous secretion to remain thick and sticky, conditions which tend to prevent sperm reaching the Fallopian tube. He treats such cases by squeezing out the corpus luteum between the 8th and 12th day after oestrus. On the other hand it is possible that the sterility of such cows might be due to partial lack of luteal tissue and therefore to deficiency of progesterone, in which case conditions in the uterus would be unfavourable for implantation of the fertilized egg. In some cases, possibly, ovulation fails to occur because of an insufficient secretion of luteinizing hormone by the anterior pituitary. Either of these conditions might be expected to benefit by treatment with P.U.

To test this theory an extended experiment was carried out with cows of the Reading University herd, many of which came in this category. Unfortunately, owing to circumstances connected with farm management, the selection of cows for treatment was not made at random. The basis of selection was as follows: most of the cows which were thought to be somewhat refractory were treated, and, in addition, a proportion of the rest of the herd—particularly at periods when it was specially desired to get cows in calf. The treatment adopted consisted of three intramuscular injections of 2 c.c. P.U. given at 2-day intervals, beginning on the day of service. The experimental period was a little greater than a year, so that seasonal variations in fertility are compensated to a large extent.

In the following treatment of the results, the services of the experimental cows are classified as treated and untreated. Included in the category of treated services are not only the services at which the P.U.

injections were given but also the subsequent services, provided that the latter occurred within the normal period of the bovine oestrous cycle. For the purposes of this analysis the limit was arbitrarily set at 28 days. This procedure was adopted because in cases where the treated service proved sterile it seemed likely that the events of the whole of the subsequent oestrous cycle, including those associated with the next oestrus, would be affected by the treatment. The results are summarized in Table I, which refers to the whole of the experimental period.

Table I

	Total no.	No. effective	Percentage effective
Experimental cows:			
All services	59	19	32·2
Treated services	30	17	56·7
Untreated services	29	2	6·9
Control cows, all services	59	34	57·6
Control and experimental cows, all services*	118	53	44·9

* The average percentage of effective services for the herd in question over the 4-year period 1935–8 was 44.

Comparison of the effective percentages of all services of experimental cows (32·2) with those of treated services only (56·7) and untreated services (6·9) indicates that the services at which the P.U. injections were given, together with the subsequent ones, were much more effective than the untreated services. Further, the proportion of the treated services, which were effective, in the case of the experimental cows, was approximately equal to the proportion of effective services of the control cows. If we assume that the experimental group was on the whole more refractory than the control group (and this was to be expected from the method of selection of cows for treatment) this would again indicate that the P.U. treatment increased the fertility of the experimental cows.

The fact that the experimental group was on the whole more refractory than the control group can be compensated for to some extent by eliminating from both groups all cows which became pregnant at the first service after calving. This method of analysis has the further advantage that it is confined only to cows to which the treatment would be

Table II

	Effective	Ineffective	Totals	Percentage effective
Treated services	10	13	23	43·5
Untreated services	2 + 9*	27 + 25*	63	17·5
Totals	21	65	86	24·4

* Control cows.

applied in practice, namely, those which were refractory in some degree. The results for such cows are summarized in Table II, in which the untreated services of the experimental cows are added to the services of the control cows.

For this four-entry table $\chi^2 = 6 \cdot 18$ and $P = 0 \cdot 013$, a highly significant result, from which it may be concluded that the treatment was particularly beneficial in the case of cows which had failed to hold to at least one service.

The fact that P.U., injected at the time of service, brought about an improvement in the fertility of cows which persistently "returned to the bull" supports the theory that in many cases this condition may be due either to failure to ovulate at oestrus or to the existence after ovulation of uterine conditions unfavourable to the implantation of the fertilized egg. The latter condition might well result from deficiency of the luteal hormone, progesterone. The partial success of the P.U. treatment supports the belief that this form of sterility may be due to either of two opposite causes, namely, on the one hand, over-abundance of anterior pituitary lutenizing hormone or, on the other, a deficiency of this secretion. The frequent operation of the first of these causes is illustrated by the fact that Hammond (private communication) has often successfully treated cows which "return to the bull" by squeezing out the corpus luteum and thereby reducing the amount of luteal tissue in the ovary.

Summary

1. The fertility of three sterile bulls was restored by injections of human pregnancy urine extract (P.U.).

2. Cows which failed to exhibit oestrus were treated by injections of P.U. Three out of five cows responded within 24 hours to intravenous injections of 5 c.c. P.U. (2500 rat units) and one out of four to an injection of 3 c.c. P.U.

Two out of five cows responded immediately to a series of three intramuscular injections of 2 c.c. P.U. and one cow responded to a single intramuscular injection of 2 c.c. P.U. In addition four cows failed to respond immediately to four intramuscular injections of 2 c.c. P.U.

3. Evidence was obtained which shows that treatment with P.U. at the time of service increases the fertility of cows which show regular oestrus but nevertheless fail to conceive. It is believed that this condition is often due (a) to failure to ovulate, and (b) to deficiency of progesterone following ovulation.

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REFERENCES

Aberle, S. B. D. & Jenkins, R. H. (1934). *J. Amer. med. Ass.* **103**, 314.

Brouha, L. & Simonnet. H. (1929). *C. R. Soc. Biol., Paris,* **101**, 368.

Dairy Husbandry Dept., Nat. Inst. Res. Dairying (1933). *Yearb. Berks Milk Rec. Soc.*

Day, F. T. (1939). *J. Agric. Sci.* **29**, 459.

Engle, E. T. (1929). *Anat. Rec.* **43**, 187.

—— (1932). *Endocrinology,* **16**, 513.

—— (1939). *Sex and Internal Secretions.* Ed. E. Allen, 2nd ed. London, chap. xviii.

Hammond, J. (1939). *Vet. Rec.* **51**, 1137.

Moore, C. R. (1928). *J. exp. Zool.* **50**, 455.

Moore, C. R. & McGee, L. C. (1928). *Amer. J. Physiol.* **87**, 436.

Weber, E. (1911). *Arch. wiss. prakt. Tierheilk.* **37**.

Zawadowsky, M. M., Eskin, I. A. & Ovsjannikov, G. F. (1935). *Trud. Dinam. Razvit. Moscow,* **9**, 75.

CLINICAL AND EXPERIMENTAL OBSERVATIONS ON REPRODUCTION IN THE MARE

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(With One Text-figure)

INTRODUCTION

IT has been shown that infertility in mares is of common occurrence. Sanders (1926), investigating the returns for premium stallions, found that the average fertility in mares was only 59% in heavy horses and 53% in light horses; Nielsen (1928) found that in Denmark the average fertility was 65%.

Scientific investigations into the physiology of reproduction in the mare have been undertaken in different countries, and it would appear that the main factors contributing to the low fertility may be summarized as: shortness of the breeding season; the irregularities in the oestrous cycle of the mare; the long duration of oestrus resulting in difficulty in judging the correct time of mating, i.e. close to the time of ovulation; and the cases of stallions of low fertility.

Many of the observations with important bearings on the control of sterility in mares have been made within recent times. The following are of special interest and importance and show the type of progress that has been made in the study of the subject, and in addition, serve as an introduction to the observations of the writer recorded in this paper.

Caslick (1937) points out the difficulty of getting mares in foal in a short breeding season, when parturition occurs towards the end of that season, and shows that on the average in a well-managed stud, matings in three oestrous periods are required for each pregnancy.

The long duration of oestrus has been observed by many workers. Hammond (1934) found oestrus normally lasted 7 days with variations from 3 to 41 days, and that if follicles were ruptured per rectum during oestrus, oestrus only lasted just under or just over 24 hr. Observations on mares killed at different times in oestrus showed that ovulation occurred within about 24 hr. of the end of oestrus. Additional evidence that ovulation occurred just before the end of oestrus was shown by

the increasing fertility of matings made towards the end of oestrus (Hammond, 1934).

McKenzie & Andrews (1937) reported the average length of oestrus to be 5·54 days with a range of 1–27 days, ovulation occurring 0·86 day before the end of oestrus, and varying from 7 days before the end of heat to 2 days after the end of oestrus. Krat (1933) found the mean duration of oestrus to be 4·96 days, and Constantinescu & Mauch (1936), 4·52 days with a range of 1–16 days. Caslick (1937) found oestrus varied from 1 to 103 days but most mares had oestrous periods of 2–6 days.

The length of dioestrus is more constant than oestrus, Hammond (1934) reported the average as 16 days. McKenzie & Andrews (1937) found it to be 15·26 days with a range of 6–29 days.

Zivotkov, Goncarenko & Krivoscekov (1936) found that ovulation occurred 1–2 days before the end of oestrus, and that matings 4–48 hr. before ovulation all gave good results (80·5% fertility).

Hammond (1938) found that the maximum fertility occurred from matings on the second day from the end of heat and that the fertility decreased as matings were made earlier or later in oestrus.

Kedrov (1938a) found inseminations from 24 hr. before ovulation to 8 hr. after ovulation gave good results, but were unsatisfactory earlier than 40 hr. before ovulation.

Kedrov (1938b) also found that rectal palpation to determine the time of ovulation in order to decide the time of mating was very useful in long-oestrus mares. He has reported degeneration of follicles after reaching ovulation size, and stresses the importance of good feeding and husbandry as essential to overcoming these long heat periods.

McKenzie & Andrews (1937) found that the average size of follicles on the first day of oestrus was 2·7 cm. and ovulation size 3·2–3·8 cm. If oestrus lasted longer than usual, follicles tended to be larger at the time of ovulation, 4·0 cm. on the seventh day, and 5·0 cm. on the eighth day.

McKenzie & Andrews (1937) and Mirskaja & Salzman (1935) found that if follicles were very small on the first day of heat (1·0 cm.) then oestrus was usually of long duration.

Ovulation has been observed in mares without the occurrence of oestrus (McKenzie & Andrews, 1937; Hammond, 1934; Mirskaja & Salzman, 1935; Caslick, 1937).

Oestrus may also occur without ovulation (Caslick, 1937; Kedrov, 1938b; Day, 1939b).

To overcome the irregularity in the length of oestrus, Mirskaja & Petropavlosky (1938) showed that injections of 1000 mouse units of

prolan on the first day of heat in mares, resulted in ovulation in 30–48 hr., and that oestrus lasted 1·4–1·6 days after ovulation. The resulting fertility from matings in these artificially shortened oestrous periods was 77·8 and 83·8%. This result compares more than favourably with normal matings as described by Constantinescu & Mauch (1936), where a single mating on the first to the third day of heat resulted in only 40·2% fertility, and two matings in one heat produced 52% fertility. When two matings were made, with the first between the first and third days and the second between the fourth and fifth days, the fertility percentage rose to 57. Kedrov (1939) found that ovulation occurred more often in the left ovary and that the foetus as palpated in pregnancy diagnosis was more often in the right horn of the uterus, thus suggesting intra-uterine migration of the ova.

The details of the mares given in this paper correspond with most of these findings, and additional information is given on some points.

The original idea of the investigation was to observe the effect of gonadotrophic hormones on the oestrous cycle of the mare, but arising out of this, observations were also made on the oestrous cycle, the changes in the ovaries, the time of ovulation in relation to length of oestrus, fertility in regard to time of mating and ovulation; and palpation of the embryo in early stages of pregnancy. The observations made on early pregnancy by means of rectal palpation of the uterus should have a useful application in the early diagnosis of pregnancy. The other methods of diagnosing pregnancy are not referred to here as they have been dealt with in other publications (Miller & Day, 1939, 1940).

MATERIALS AND METHODS

The work now to be recorded gives details of the oestrous cycles of eight pony mares during the 1939 breeding season, commencing with all mares in anoestrus in the early spring, until they became pregnant in the summer. Clinical observations have been made on changes in the ovaries during the cycle, the time of ovulation in oestrus, and the time of mating in relation to fertility. A description is also given of the clinical examination of the developing foetus in early pregnancy and of changes in the ovaries and the oestrous cycle following injections of various gonadotrophic hormones.

Of the eight mares used six were Welsh ponies, one a New Forest pony, and one a Shetland pony.

Five Welsh ponies, A, B, C, D and E, were pregnant in 1938, but the

foetuses were removed during August 1938, at the 51st to 105th days of pregnancy, as judged by foetal measurements.

The other Welsh pony (F) and the New Forest pony (G) had foals late in the summer of 1938 and were not mated again in that year.

The histories of all these mares (except the Shetland) until they went into anoestrus in November 1938 have been published. Mares A, B, C, D and E correspond to mares 1, 3, 4, 5 and 7 respectively (Day, 1939a), and mares F and G correspond to mares 8 and 6 (Day, 1939b) in previous publications. The Shetland mare H had a foal in 1938, and was not mated again in that year.

The mares were tried daily with a vasectomized stallion to determine their oestrous periods, and rectal palpation was carried out as often as necessary to follow changes in the ovaries during the oestrous cycle and changes in the uterus during pregnancy.

Vaginal examinations were made with a speculum to observe changes in the vagina and cervix in the oestrous cycle, in pregnancy and anoestrus.

Mares were injected with different hormone preparations. Various doses were given, either intravenously or subcutaneously, and the subsequent changes were followed in the ovaries.

At the end of the 1939 summer the mares were inseminated at different times in oestrus to determine the optimum time for fertility in relation to time of ovulation and the duration of oestrus. The sperm for insemination was collected by means of an artificial vagina from an aged pony stallion. The seminal fluid was separated from the sperm as described by Walton (1938) and different volumes of sperm were inseminated. Sperm counts were taken to determine the density, so that an estimation of the total number of sperm inseminated could be made. The artificial vagina used was designed by McKenzie (1938).

THE OESTROUS CYCLE

In Table I, the results are given of the length of oestrus and dioestrus, the ovary which ovulated at each oestrus, and the time of ovulation in relation to the end of the oestrus. The time of the year and the oestrous periods in which the mares became pregnant are also given.

Length of oestrus. The length of oestrus varied according to the time of year and there was a slight individual variation in the different mares.

As a rule oestrus lasted longer in the early spring, 11–20 days and in one case 54 days, whereas in the middle of summer it varied in

individual mares from 4 to 9 days; in the majority of cases oestrus lasted about 7–8 days.

Length of dioestrus. This varied from 5 to 30 days, but in most cases was 12–16 days. The longer periods occurring in the early spring. Again, there was an individual variation, some mares averaging 11–14 days and others 14–16 days.

Dioestrous periods of under 11 days occurred only after oestrous periods in which ovulation had not taken place.

Table I

Mare	Dates	Length of dioestrus (days)	Length of oestrus (days)	Active ovary	Time between ovulation and end of oestrus (days)
A	7–21 March	—	15	Left	No ovulation
	22–27 March	5	—	—	—
	27 March–17 April	—	22	Left	2
	18 April–14 May	27	During this dioestrus, 5 days, on which mare showed oestrus to teaser		
	15–21 May	—	7	Right	2
	22 May–2 June	11	—	—	—
	2–8 June	—	7	Left	2
	8–19 June	11	—	—	—
	20–23 June	—	4	Right	2
	24 June–7 July	14	—	—	—
	8–14 July	—	7	Right	Under 1

Pregnant to insemination on 5th day of this oestrous period (48 hr. before ovulation)

Mare	Dates	Length of dioestrus (days)	Length of oestrus (days)	Active ovary	Time between ovulation and end of oestrus (days)
B	3–9 April	—	7	Left	1
	10–26 April	16	—	—	—
	26 April–8 May	—	13	Right	1
	8–23 May	15	—	—	—
	23 May–4 June	—	13	Right	4
	4–17 June	13	—	—	—
	17–21 June	—	5	Right	Under 1
	22 June–4 July	13	—	—	—
	5–10 July	—	6	Left	Under 1

Pregnant to insemination on 3rd day of this oestrous period (72 hr. before ovulation)

Mare	Dates	Length of dioestrus (days)	Length of oestrus (days)	Active ovary	Time between ovulation and end of oestrus (days)
C	20 April–9 May	—	19	Left	1 (after end of oestrus)
	10–25 May	15	—	—	—
	25–31 May	—	7	Right	Under 1
	1–13 June	13	—	—	—
	14–16 June	—	3	Right	Under 1
	17 June–2 July	16	—	—	—
	3–10 July	—	8	Right	Under 1

Pregnant to insemination on 5th day of this oestrous period (72 hr. before ovulation)

Mare	Dates	Length of dioestrus (days)	Length of oestrus (days)	Active ovary	Time between ovulation and end of oestrus (days)
D	9–12 March	—	4	Left	No ovulation
	13 March–11 April	30	—	—	—
	12 April–1 May	—	20	Right	5
	2–13 May	12	—	—	—
	14–21 May	—	8	Left	2
	22 May–4 June	14	—	—	—
	5–11 June	—	7	Right	1
	12–26 June	15	—	—	—
	27 June–1 July	—	5	Left	Under 1

Pregnant to insemination on 4th day of this oestrous period (24 hr. before ovulation)

Table I (continued)

Mare	Dates	Length of dioestrus (days)	Length of oestrus (days)	Active ovary	Time between ovulation and end of oestrus (days)
E	24–28 April	—	5	Right	1 (after end of oestrus)
	29 April–18 May	20	—	—	—
	19–22 May	—	4	Left	Under 1
	23 May–7 June	16	—	—	—
	8–10 June	—	3	Left	Under 1
	11–26 June	16	—	—	—
	27–30 June	—	4	Right	Under 1

Pregnant to insemination on 3rd day of this oestrous period (24 hr. before ovulation)

F	15–21 March	—	7	Left	No ovulation
	22 March–18 April	28	—	—	—
	19–30 April	—	12	Right	No ovulation
	1–5 May	5	—	—	—
	6–16 May	—	11	Left	Under 1
	16–30 May	14	—	—	—
	31 May–8 June	—	9	Right	1
	9–22 June	14	—	—	—
	23–30 June	—	8	Left	Under 1
	1–16 July	16	—	—	—
	17–25 July	—	9	Left	1
	26 July–6 August	12	—	—	—
	7–14 August	—	8	Right	1

Pregnant to insemination on 5th day of this oestrous period (48 hr. before ovulation)

G	13 March–6 May	—	54	Left at beginning, but ovulation in right	Under 1

Mare did not show to teaser on 6 odd days during this oestrus

	7–22 May	16	—	—	—
	23–29 May	—	7	Left	Under 1
	30 May–14 June	16	—	—	—
	15–22 June	—	7	Right	1
	23 June–7 July	15	—	—	—
	8–16 July	—	8	Right	Under 1

Pregnant to insemination on 7th day of this oestrus (24 hr. before ovulation)

H	25 August–1 Sept.	—	7	—	—

Pregnant as a result of mating on each day in oestrus

In one mare (A), signs of oestrus occurred on 5 days during a 27-day dioestrus, but the first of these days on which the mare showed such signs was the twelfth day of the cycle, and the duration of the abnormal oestrus in each case did not exceed 1 day, and was alternated by intervals of 2 or 3 days on which the mare failed to show signs of oestrus.

CHANGES IN THE OVARIES DURING THE OESTROUS CYCLE

In describing the changes in the ovaries, the size of follicles is given in centimetres diameter. These measurements are assessed by palpating the ovary and judging relative sizes of follicles in the same way that coins of different denominations can be picked out of the pocket.

Before any of the mares came into oestrus follicles developed in one or both ovaries, varying in size from 1·0 to 1·5cm., and these could be palpated in all mares for about 14–30 days before they first showed symptoms of oestrus at the onset of the breeding season.

At the commencement of oestrus usually two or three, and sometimes more, follicles came up in one or both ovaries, and on the first day of oestrus varied in size from 1·0 to 3·0 cm. If there was a 3·0 cm. follicle on the first day, it was usually the only one present, whereas when the largest was 1·5 cm., there was often a number present in both ovaries.

In the oestrous periods which lasted up to 8 or 9 days, usually by the third day one follicle had increased in size to 2·5–4·0 cm., usually about 3·0 cm., and as this follicle matured to ovulation size the other follicles regressed, although occasionally two follicles would develop to ovulation size. The size at which follicles ovulated varied from 3·0 to 5·0 cm., usually about 4·0 cm. When follicles were increasing in size during oestrus, they felt very tense to the touch and did not fluctuate, but in the 24 hr. prior to ovulation, there was a decrease in the intra-follicular pressure and the follicles felt much softer, somewhat like a flabby blister.

After ovulation the collapsed walls of the follicle felt soft and flabby and an indentation could be felt on the surface of the ovary. Within about 8 hr. after ovulation the collapsed walls of the follicle were redistended by blood which accumulated in the cavity of the follicle and at this stage the ovary felt soft and spongy. In the next 24 hr. there was a gradual hardening of the freshly formed corpus luteum and by 72 hr. after ovulation the corpus luteum could no longer be distinguished from the rest of the ovarian tissue.

During the long oestrous period of 54 days (mare G) the largest follicles in the first half of oestrus were in the left ovary, but towards the end of oestrus a follicle came up and ovulated in the right ovary.

By the time ovulation occurred the smaller follicles, which were developing early in oestrus, had usually regressed, and even when a second follicle had come up to ovulation size, this usually diminished in size very rapidly after the formation of a corpus luteum, and as a rule no palpable follicles were present in the ovaries between the interval of 3–10 days after ovulation.

OVULATION

In the early spring there were four oestrous periods relating to three mares in which ovulation did not occur. But after the first oestrous period in which they ovulated, ovulation took place in all subsequent oestrous periods.

The time of ovulation in relation to the end of oestrus was fairly constant, although there was a slight variation in different mares.

Table II shows the total numbers of ovulations in all mares and the day on which ovulation took place in relation to the end of oestrus.

Table II

Days before and after end of oestrus	Before end					Last day of oestrus	After end
	5	4	3	2	1	0	1
No. of ovulations	1	1	- -	5	7	15	2

Out of 31 ovulations, 27 occurred within 48 hr. before the end of oestrus, 2 one day after the end of oestrus, and 2 on the fourth and fifth days before the end of oestrus.

As shown in Table I, ovulation does not occur alternately in the left and then the right ovary, but the frequency of ovulation in either ovary is approximately equal. In these mares, the left ovary ovulated 13 times to 18 times in the right ovary.

FERTILITY FOLLOWING INSEMINATION AT DIFFERENT TIMES IN RELATION TO THE TIME OF OVULATION

Mares were inseminated, and the ovaries palpated at frequent intervals to determine the exact time of ovulation.

Table III shows that inseminations within 72 hr. before the time of ovulation are equally good for fertility, whereas inseminations in the interval of 2–4 hr. after ovulation were not effective.

Table III

	Before ovulation			After ovulation	
Time in hours	72	48	24	2	4
No. of mares inseminated:					
Pregnant	2	2	3	—	—
Barren	1	1	2	2	2

RECTAL EXAMINATION OF THE UTERUS IN EARLY PREGNANCY

After the mares were inseminated, rectal examinations of the uterus were made at intervals of 3 days until the developing foetus could be palpated.

Before the foetus could be palpated it was usually possible to anticipate that the mare would be pregnant by the tone of the uterus at the 15th day after the ovulation giving rise to the pregnancy.

When the mares were barren, the uterus felt quite soft and flaccid, whereas in early pregnancy it became quite turgid. To the touch, the differences can be described as like a fold of velvet cloth in the case of
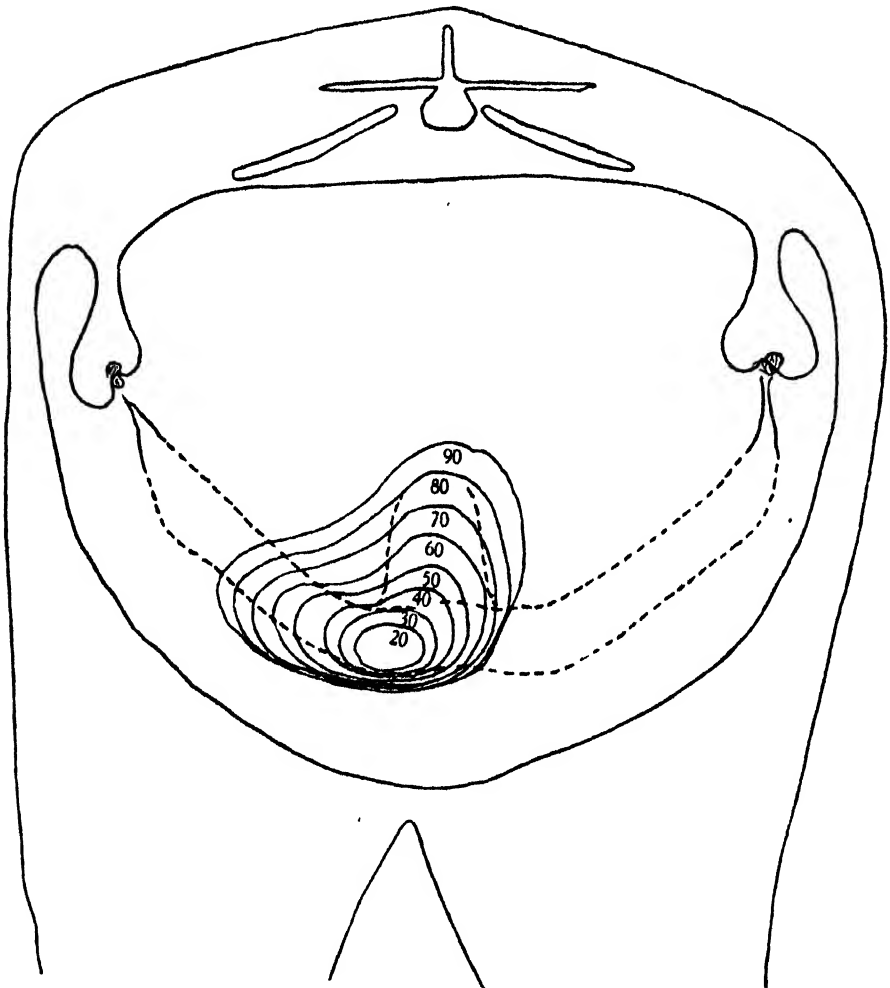
Fig. 1. Antero-posterior view of non-pregnant uterus *in situ*, showing relative sizes of developing foetus and membranes at different stages of pregnancy. The numbers in the figure are the days of pregnancy.

the barren mare, whereas in pregnancy it feels like a piece of pressure tubing.

In one mare the foetus was first detected at the 16th day, and in the other six mares on the 20th, 21st, 22nd and 23rd days of pregnancy respectively, dating the pregnancy from the time of ovulation and not from the time of service, which on the average was 2 days earlier.

In all these cases the foetus was first palpated in the same position, viz. in the horn of the uterus just above the bifurcation of the two horns, and at the stage of 16–20 days its size and consistence were that of a shelless bantam's egg.

Table IV gives the relative sizes of the developing foetus at different stages of pregnancy and Fig. 1 is a diagrammatic representation of the position and size of the foetus in relation to the size of the non-pregnant uterus.

Table IV

Stage of pregnancy in days	Size of foetus	Position of foetus
16	Bantam's egg	In uterine horn just above junction of uterine horn and body
20	Golf ball	
25	Pheasant's egg	
30	Hen's egg	
35	Tennis ball	
40	Turkey's egg	
45	Goose egg	
50	Jaffa orange	Occupying $\frac{2}{3}$ of uterine horn and $\frac{1}{4}$ of body of uterus
60	Jaffa orange	„ „
70	Ostrich egg	Occupying uterine horn and $\frac{1}{4}$ uterine body

In five of the seven mares the foetus developed in the opposite horn of the uterus to the ovary in which the ovulation of pregnancy occurred, and in the other two mares it developed in the same side. In one mare (B) ovulation occurred on the 23rd day of pregnancy, but the mare did not show any signs of oestrus.

Table V

Designation of mare	Ovary in which ovulation occurred	Uterine horn in which foetus developed
A	Right	Left
B	Left	Right
C	Right	Right
D	Left	Right
E	Right	Left
F	Right	Right
G	Right	Left

THE EFFECT OF INJECTIONS OF GONADOTROPHIC HORMONES
ON THE OESTROUS CYCLE OF MARES

In Table VI are recorded the details of all injections given to eleven pony mares from August 1938 to September 1939.

The results of these injections may be summarized as follows: Doses of 1000–2000 mouse or rat units of pregnancy urine extract when given intravenously induced ovulation in 20–40 hr. in most mares, independent

of the time in oestrus at which the injection was given, and the length of oestrus was shortened correspondingly (B, 6 April 1939; C, 6 May 1939, 14 June 1939; E, 27 April 1939, 9 June 1939; G, 4, 27 September 1938; Broke, 16 September 1938). There should be a useful application for this treatment in mares having long heat periods during the early spring, particularly as the time of mating could then be arranged so as to offer the maximum chances of fertility. Ovulation did not occur when the size of follicles was small at the time of injection (A, 6 April 1939; C, 31 August 1938; F, 13 September 1938; G, 6 April 1939), and on two occasions with mare F (24 September 1938, 27 April 1939) and on one occasion with mare C (24 July 1939) this dosage failed to induce ovulation, although follicles were sufficiently large.

Pregnant mare serum extract given in doses of 500–1000 mouse units on 3 or 4 successive days usually induced oestrus on the last day of injection or within an interval of 3 days after the last injection (B, 27 March 1939; E, 22 April 1939). When injections were commenced at the 10th-13th day of dioestrus the onset of oestrus was not hastened nor was the length of the following oestrus shortened (D, 12 May 1939; E, 2 June 1939; F, 26 May 1939; G, 8 June 1939). In most cases the oestrus following injection was of normal duration and ovulation occurred. In two cases (D, 8 March 1939; G, 11 October 1938) the mares came in oestrus and the follicle increased in size, but ovulation did not occur; both these cases were close to the anoestrum.

Horse pituitary extract in doses of 50-200 mg. subcutaneously usually induced oestrus in 2 or 3 days (F, 20 May 1939; H, 22 August 1939), and if given at the onset of oestrus ovulation was hastened and oestrus shortened (A, 20 June 1939). It is interesting to note that mare H, the only mare which was mated to a stallion in an induced oestrous period, became pregnant.

The continual injection of all these hormone preparations had no deleterious effect on the subsequent oestrous cycles of any of the mares, as all of them which were mated afterwards became pregnant.

A large group of mares in addition to those detailed here have been injected with the same hormone extract on the basis of the experience gained in these experimental mares and the results from these were more satisfactory as fewer failures occurred.

None of the preparations given during the anoestrous period (November-March) had any effect, although up to 800 mg. of horse pituitary extract was given.

The fairly numerous negative results shown in Table VI (A, 13

October 1938; D, 3 October 1938, 22 April 1939; E, 11, 22 October 1938; F, 27 June 1939; G, 8 July 1939; Brownie, 3, 11 October 1938) can be attributed in part to the fact that the dosage required by individual mares to elicit the same response varied considerably, but, as will be noticed from the dates, the failure is mainly due to the time of year at which the injection was given, bordering on the anoestrous period of November and March. Whether this was due to the anoestrous state as such, or to the poor nutritive conditions of the mares at that time of year, was not ascertained; the mares were wintered out with hay only as feed. In any case it would not be an economic proposition to breed from mares in this country in the anoestrous period and the effects in the normal breeding season are of greater practical importance.

It is possible that the continued injection of these hormones may have resulted in the mares producing antigens against the particular extract, thus causing some of the irregular results.

SUMMARY

1. The length of oestrus in mares varied from 3 to 54 days, although in most cases it was 7–8 days.

2. The length of dioestrus varied from 5 to 30 days, but in most cases was 11-16 days.

3. Ovulation occurred in most cases on the last day of oestrus, but a considerable number of ovulations occurred on the 1st and 2nd days before the end of oestrus, and in a few cases from the 5th day before the end of oestrus to 1 day after the end of oestrus.

4. Artificial insemination of mares was equally effective in the intervals of 24, 48 and 72 hr. before ovulation but was unsuccessful in intervals of 2 and 4 hr. after ovulation.

5. Pregnancy was diagnosed in all mares by rectal palpation on the 23rd day and in one mare as early as the 16th day.

6. The foetus developed in the opposite horn of the uterus to the ovary which ovulated at the onset of pregnancy in five out of seven mares.

7. Ovulation occurred in one mare on the 23rd day of pregnancy.

8. Gonadotrophic hormones had no effect when given in the anoestrous period (November to March).

9. Ovulation was induced in 20–40 hr. in most cases after the intravenous injection of 1000–2000 mouse or rat units of pregnancy urine extract intravenously, provided a fairly mature follicle was present in the ovary at the time of injection.

When this ovulation occurred, the duration of oestrus was shortened.

Table VI

Sizes of follicles in ovaries are represented by figures giving the approximate diameter in centimetres.
Antuitrin S is a pregnancy urine extract.
Physostab is a pregnancy urine extract.
Serogan is a pregnant mare serum extract.
Antostab is a pregnant mare serum extract.
FSH is an acetone dried preparation of the anterior lobe of horse pituitaries and was injected by weight in milligrams.
i/v means intravenously.
s/c means subcutaneously.

Mare	Date	Day in oestrous cycle	Condition of ovaries	Hormone injection	Result and remarks
A (5 years)	13. x. 38	4th oestrus	No follicles	10 mg. FSH s/c	In oestrus 8 days, no follicles matured
	15. xi. 38	30th dioestrus	No follicles	500 m.u. Serogan s/c	No result
	9–13. xii. 38	Anoestrus	No follicles	50 mg. FSH s/c for 5 successive days	No result
	6. iv. 39	11th oestrus	Left ov. 2·5	500 m.u. Physostab i/v	No result, oestrus lasted 22 days, ovulation on 20th day
	20. vi. 39	1st oestrus	Right ov. 2·0	50 mg. FSH s/c	Oestrus lasted 4 days, ovulation 22 hr. after injection
			Mare became pregnant to insemination 13. vii. 39		
B (5 years)	11. x. 38	41st dioestrus	No follicles	40 mg. FSH s/c	No result
	29. xi. 38	Anoestrus	No follicles	1500 m.u. Antostab s/c	No result
	16–20. xii. 38	Anoestrus	No follicles	400 mg. FSH s/c for 5 successive days	No result
	27. iii. 39	Anoestrus	Left ov. 2·0	500 m.u. Antostab s/c	
	29. iii. 39		—	500 m.u. Antostab s/c	—
	31. iii. 39		—	500 m.u. Antostab s/c	—
	6. iv. 39	3rd oestrus	Left ov. 3·5	500 m.u. Physostab i/v	Oestrus 3 days after this injection. Ovulation 70 hr. after injection, oestrus lasted 7 days
			Mare became pregnant to insemination on 8. vii. 39		
C (6 years)	31. viii. 38	2nd oestrus	Left ov. 1·0	500 r.u. Antuitrin S i/v	In oestrus 10 days, ovulated on 10th day
	11. x. 38	33rd dioestrus	No follicles	20 mg. FSH s/c	No result
	22. x. 38	44th dioestrus	No follicles	100 mg. FSH s/c	No result
	5–8. xii. 38	68th dioestrus	No follicles	1000 r.u. Serogan s/c	No result
		Anoestrus	No follicles	2000 r.u. Antuitrin S s/c for 4 successive days	No result
	27. iv. 39	8th oestrus	Left ov. 3·0	1000 m.u. Physostab i/v	No result
	6. v. 39	17th oestrus	Left ov. 5·0	1000 m.u. Physostab i/v	Ovulation 4 days later, one day after end of oestrus, oestrus 20 days
	14. vi. 39	1st oestrus	Right ov. 3·5	1000 m.u. Physostab i/v	Ovulation 36 hr. after injection, oestrus 3 days
			Mare became pregnant to insemination on 7. vii. 39		

	Date	Stage	Follicle	Treatment	Result
D (4 years)	3. x. 38	1st oestrus	No follicles	3000 r.u. Antuitrin S s/c	In oestrus 6 days, no follicles matured
	15. xi. 38	34th dioestrus	No follicles	2000 m.u. Serogan s/c	No result
	5. xii. 38 / 6. xii. 38 / 7. xii. 38 / 8. xii. 38	Anoestrus	No follicles	500 r.u. Antuitrin S s/c for 4 successive days	No result
	14–20. ii. 39	Anoestrus	Left ov. 1·0	200 m.u. Antostab s/c for 7 successive days	No result except slight increase in size of follicle in left ovary
	8. iii. 39	Anoestrus	Left ov. 1·0 / Right ov. 1·75	800 mg. FSH s/c	Oestrus in 24 hr., remained in oestrus 4 days, did not ovulate, but follicles up to 3·0 and 3·5 cm. and these persisted
	22. iv. 39	11th oestrus	Left ov. 3·0 / Right ov. —	500 m.u. Physostab s/c	Ovulation 5 days after injection and 4 days before end of oestrus
	12–15. v. 39	11th dioestrus	Left ov. — / Right ov. —	1000 m.u. Antostab s/c on each of 4 days	Oestrus on 14. v. 39, 2 days after 1st injection, oestrus lasted 8 days, with ovulation on 6th day

Mare became pregnant to insemination on 30. vi. 39

	Date	Stage	Follicle	Treatment	Result
E (3 years)	11. x. 38	50 days since induced abortion	No follicles	10 mg. FSH s/c	No result
	22. x. 38	61 days since induced abortion	No follicles	100 mg. FSH s/c	No result
	16. xi. 38	Anoestrus	No follicles	400 mg. FSH s/c	No result
	9–13. xii. 38	Anoestrus	No follicles	100 mg. FSH s/c for 5 successive days	No result
	14–20. ii. 39	Anoestrus	No follicles	100 m.u. Antostab s/c for 7 successive days	No result, except follicle in right ov. up to 1·0 cm.
	8–11. iii. 39	Anoestrus	Right ov. 2·0	200 mg. FSH s/c for 4 successive days	No result
	22, 23. iv. 39	Anoestrus	Left ov. 1·5	500 m.u. Antostab for 2 successive days	Oestrus 1 day after last injection
	27. iv. 39	4th oestrus	Left ov. 3·0	1000 m.u. Physostab i/v	Ovulation 40 hr. later, oestrus 5 days, ovulation 1 day after end of oestrus
	2–4. vi. 39	11th dioestrus	No follicles	500 m.u. Antostab s/c for 3 successive days	Oestrus 4 days after last injection, lasted 3 days, ovulation on 3rd day
	9. vi. 39	2nd oestrus	Left ov. 2·75	1000 m.u. Physostab i/v	Ovulation in 20 hr. (see above)

Mare became pregnant to insemination on 29. vi. 39

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Table VI (continued)

Mare	Date	Day in oestrous cycle	Condition of ovaries	Hormone injection	Result and remarks
F (aged mare)	13. ix. 38	1st oestrus	Right ov. 1·5	2000 r.u. Antuitrin S i/v	In oestrus 7 days, did not ovulate follicle up to 4·0 cm., went up to 5·0 cm. by 11th dioestrus, and went down when opposite ovary ovulated in next oestrus
	24. ix. 38	5th dioestrus	Right ov. 4·5	1000 r.u. Antuitrin S i/v	No result (see above)
	29. xi. 38	15th dioestrus	No follicles	2000 r.u. Serogan s/c	No result
	14–20. ii. 39	Anoestrus	No follicles	400 m.u. Antostab s/c for 7 successive days	Follicle in right ov. up to 1·5 cm., but no result
	27. iii. 39 / 29. iii. 39 / 31. iii. 39	Anoestrus	No follicles	1000 m.u. Antostab s/c on 3 alternate days	No result
	27. iv. 39	9th oestrus	Right ov. 3·0	1000 m.u. Physostab i/v	Remained in oestrus 3 days, did not ovulate
	26–29. v. 39	10th dioestrus	No follicles	500 m.u. Antostab s/c for 4 successive days	Oestrus 2 days after last injection, lasted 9 days, ovulation 8th day
	20–22. vi. 39	12th dioestrus	Right ov. 2·0	50 mg. FSH s/c for 3 successive days	Oestrus 1 day after last injection, lasted 8 days, ovulation 8th day
	27. vi. 39	5th oestrus	Left ov. 2·0	50 mg. FSH s/c	No result (see above), ovulation 72 hr. after injection
	Mare became pregnant to insemination on 11. viii. 39				
G (4 years)	4. ix. 38	1st oestrus	Right ov. 3·0	1000 r.u. Antuitrin S i/v	Ovulation 30 hr. after injection, oestrus lasted 3 days
	27. ix. 38	1st oestrus	Left ov. 2·5	2000 r.u. Antuitrin S i/v	Ovulation 30 hr. after injection, oestrus lasted 3 days
	11. x. 38	1st oestrus	Right ov. 2·5	20 mg. FSH s/c	Mare in oestrus 8 days, follicle came up to 3·5 cm., did not ovulate and went down in dioestrus
	29. xi. 38	42nd dioestrus	No follicles	4000 r.u. Serogan s/c	No result
	16–20. xii. 38	Anoestrus	No follicles	800 mg. FSH s/c for 5 successive days	No result

Animal	Date	Oestrus state	Ovary/follicles	Treatment	Result
	6. iv. 39	24th oestrus	Left ov., several follicles up to 2·5; Right ov., several follicles up to 1·5	500 m.u. Physostab i/v	No result
	8–10 vi. 39	10th dioestrus	No follicles	1000 m.u. Antostab s/c for 3 successive days	No result, oestrus 5 days after last injection, oestrus lasted 8 days, ovulation 7th day
	8. vii. 39	1st oestrus	Right ov. 2·5	50 mg. FSH s/c	No result, oestrus lasted 8 days, ovulation 8th day, mare became pregnant to insemination in this oestrus
			Mare became pregnant to insemination on 15. vii. 39		
H (aged mare)	22. viii. 39	Not in oestrus in 1939	Right ov. 2·0	100 mg. FSH s/c	Oestrus 3 days later, oestrus lasted 8 days and mare was covered each day
			Mare became pregnant to services in this oestrus, 25. viii.–2. ix. 39		
Broke (aged mare)	16. ix. 38	1st oestrus	Right ov. 3·0	1000 r.u. Antuitrin S i/v	Ovulation 30 hr. after injection, oestrus lasted 3 days
	16. x. 38	28th dioestrus	No follicles	100 mg. FSH s/c	No result
	20. x. 38	32nd dioestrus	No follicles	200 mg. FSH s/c	No result
	16. xi. 38	Anoestrus	No follicles	400 mg. FSH s/c	No result
	9–13. xii. 38	Anoestrus	No follicles	100 mg. FSH s/c for each of 5 successive days	No result
	6–8. i. 39	Anoestrus	No follicles	500 m.u. Serogan s/c for 3 successive days	No result
	10. i. 39	Mare destroyed	No follicles	—	
Brownie (4 years)	3. x. 38	47th dioestrus	No follicles	4000 r.u. Antuitrin S s/c	Came in oestrus in 5 days
	11. x. 38	4th oestrus	No follicles	20 mg. FSH s/c	Remained in oestrus 4 more days, no follicles matured
	16. xi. 38	32nd dioestrus	No follicles	800 mg. FSH s/c	No result
	9–13. xii. 38	Anoestrus	No follicles	200 mg. FSH s/c for each of 5 successive days	No result
	23. i. 39	Mare died	No follicles in ovaries, but one very small C.L. about 0·5 × 0·5 cm.		
May (5 years)	14. x. 38	61 days since induced abortion	No follicles	200 mg. FSH s/c	No result
	20. x. 38	—	No follicles	100 mg. FSH s/c	No result
	5–8. xii. 38	—	No follicles	2000 r.u. Antuitrin S s/c for 4 successive days	No result
	24. i. 39	Mare was destroyed			

10. Oestrus was induced by the injection of 500–1000 mouse units of pregnant mare serum extract given subcutaneously for 3 days or more. When given at 10th–13th day of dioestrus, the normal dioestrous period was not shortened.

11. Horse pituitary extract in doses of 50–100 mg. induced oestrus in a few days, and when given at onset of oestrus hastened ovulation and shortened oestrus. The only mare mated in an induced oestrus became pregnant.

12. Continued injection of gonadotrophic hormones did not have any deleterious effect on the subsequent oestrous cycle of mares and did not prevent them from becoming pregnant afterwards.

REFERENCES

CASLICK, E. A. (1937). *Cornell Vet.* **27**, 187–206.
CONSTANTINESCU, C. K. & MAUCH, A. (1936). *Ann. Inst. Nat. Zootechnique Roumanie,* **5**, 9–78.
DAY, F. T. (1939a). *J. agric. Sci.* **29**, 459–69.
—— (1939b). *J. agric. Sci.* **29**, 470–5.
HAMMOND, J. (1934). *Actes de 16th Congrès Internaticnale d'Agriculture, Budapest.*
—— (1938). *Trans. Yorks. agric. Soc.* **95**, 11–25.
KEDROV, V. K. (1938a). *Probl. Zivota,* no. 3, 55–65.
—— (1938b). *Probl. Zivota,* no. 4, 151–5.
—— (1939). *Dokl. seljskahaz Nauk,* no. 2/3, 65–7.
KRAT, A. V. (1933). *Konevodstvo,* no. 1, 55–9.
MCKENZIE, F. F. & ANDREWS, F. N. (1937). *Proc. Amer. Soc. Anim. Prod.* **30**, 64.
MCKENZIE, F. F. (1938). Personal Communication.
MILLER, W. C. & DAY, F. T. (1939). *J. R. Army vet. Cps,* **10**, 95–105.
—— —— (1940). (In the Press.)
MIRSKAJA, L. M. & SALZMAN, A. A. (1935). *Advance of Zootechnical Sciences (Moscow),* **1** (1), 157–68.

MIRSKAJA, L. M. & PETROPAVLOSKY, V. V. (1938). *Cornell Vet.* **28**, 58–61.

NIELSEN, F. (1928). *Festskrift Bernhard Bang, Copenhagen,* p. 323.

SANDERS, H. G. (1926). *J. agric. Sci.* **16**, 466.

WALTON, A. (1938). *Proc. Amer. Soc. Anim. Prod.* **31**, 238.

ZIVOTKOV, H. I., GONCARENKO, K. S. & KRIVOSCEKOV, A. G. (1936). *Probl. Zivota,* no. 3, 71–6.

THE ESTIMATION OF THE YIELDS OF CEREAL EXPERIMENTS BY SAMPLING FOR THE RATIO OF GRAIN TO TOTAL PRODUCE

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1. INTRODUCTION

THRESHING difficulties constitute a formidable barrier in planning an extensive series of small-plot cereal experiments of modern design, or in studying the residual effects of treatments on the succeeding cereals in a series of experiments on root crops. Failing the provision of a small threshing machine, sampling is at present the only practicable method for obtaining the grain yields of small plots located on commercial farms.

Yates & Zacopanay (1935) summarized the work carried out at Rothamsted and its associated outside centres on the estimation of the yields of cereal crop experiments by sampling. In these experiments a number of small areas (e.g. $\frac{1}{2}$ m. of each of four contiguous rows) were selected at random in each plot or subplot. The standing crop in each of these areas was cut close to the ground, bagged, and transported to Rothamsted for threshing, the yields of grain and straw per unit area being estimated entirely from the samples.

The authors suggested that, if the total produce of each plot were weighed on the field, the samples need be used only to determine the ratio of the weight of grain to the weight of total produce. In view of the high correlation which normally exists between grain and straw yields, the sampling errors of this ratio might be expected to be considerably smaller than those of the yield of grain itself, so that less sampling would be required to obtain results of equal precision. They found from the average of nine experiments that the sampling error per metre of row length was 7·14 % for the ratio of grain to total produce, compared with 23·9 % for the yield of grain. Judging from these figures, only about one-tenth of the number of samples is required to obtain equal information if the total produce is weighed. The estimation of yields by this method has been tried in a number of experiments since 1935. The

present paper reviews their results from the point of view of sampling technique.

Since total produce, when weighed on the field, usually contains some moisture, the samples must be weighed on the field as well as before threshing, to enable a correction to be made in the grain and straw figures for the loss of moisture. If the samples are taken from the standing crop, this should be done immediately before the crop is reaped, in order that the samples and the total produce may be weighed on the field at the same time. This may not always be convenient, but with this method the samples can alternatively be taken from the crop while it is lying in the stooks, since there is no need to know the area of the land from which a sample was taken. As the crops usually lie in the stooks for some days, this gives a wider choice in the time during which the sampling must be carried out. In most of the experiments discussed below, the samples were taken from the stooks.

2. Method of sampling from the stooks

Total produce is first weighed on each plot. A spring balance may be used, weighing the sheaves one at a time. This method is rather tedious unless the plot size is small or the crop is a poor one, since a 1/40 acre plot may contain thirty sheaves. If a portable tripod is available with a platform which can hold all the sheaves in one stook, some time will be saved. After weighing, the sheaves should be laid separately on the ground, to facilitate the sampling operations.

The next step is to select the samples. A method which gives reasonably random samples is as follows: Suppose that there are eighteen sheaves on a plot and that each sample is to be approximately 1% of the produce of the plot. A sheaf is first selected at random. The binding tape is cut and the sheaf is divided into six portions of about equal weight. One of these is selected at random and constitutes the sample. The division of the sheaf is usually most quickly done by successive subdivision into halves, selecting one-half at random at each stage for further subdivision, until a sample of about the required size is reached. This method also has the advantage that it reduces to a minimum the number of small bundles which are scattered about the plot. For selecting the halves at random, a piece of paper bearing a selection of odd and even numbers drawn from a book of random numbers may be used; alternatively, a set of disks containing an equal number of two different colours may be carried in the pocket.

When the samples have been selected, labelled and bagged, they are weighed. For the calculation of the grain yields on each plot, it is necessary to know only the *total* weight of the samples from the plot, but if a full investigation of sampling errors is required, each sample must be weighed individually. As the samples may weigh less than one pound each, a fairly accurate balance is required, and the weighings should if possible be done indoors whenever there is any appreciable wind. The average weight of a bag, with its label and string, must also be recorded.

This completes the experimental operations on the field. The sheaves should be restooked unless they are being carted off immediately.

The taking of random samples from the stooks is a lengthy process. Following a suggestion made by Yates & Zacopanay, samples were also taken by picking a few shoots from each of several sheaves until a sample of about the agreed size had been amassed. These samples, which will be called grab samples, can be taken in about one-third of the time required for random samples, since the sheaves need not even be opened unless they are very tightly bound. It is, however, not clear *a priori* whether grab samples give unbiased estimates of the grain/total produce ratios or how they compare in accuracy with random samples. In grabbing, no attempt was made to select representative shoots, as this method is known to be likely to introduce bias. One might, however, expect a tendency to miss the shorter and less vigorous shoots, and possibly also to free the shoots of weeds in pulling them from the sheaves. Both factors would tend to increase the apparent grain/total produce ratio. A comparison of the results with random and grab samples will be given later in this paper.

3. MATERIAL

A list of the experiments discussed is given in Table I below. The plots were not subdivided for sampling, so that the plot area given is in all cases the area to which the sampling errors apply.

The random samples were taken from the stooks in five experiments. The grab samples were taken from the stooks in all cases except in exp. 5, where they were taken from the crop as it lay on the ground immediately after scything.

Table I. *List of experiments*

No.	Year	Place	Type	Size of plot acres	Random samples taken from	No. of samples per plot Random	Grab
			Wheat				
1	1935	Rothamsted	6 × 6 L.S.*	1/40	Stooks	2	1
2	1935	Woburn	6 × 6 L.S.	1/100	Stooks	2	1
3	1936	Woburn	6 × 6 L.S.	1/100	Standing crop	2	1
			Barley				
4	1936	Rothamsted	4, 16 R.B.†	1/40	Stooks	2	1
5	1937	Wye	6 × 6 L.S.	1/120	Standing crop	2	2
6	1937	Tunstall	3, 9 R.B.	1/40	Stooks	2	2
			Oats				
7	1938	Rothamsted	4, 18 R.B.	1/60	Stooks	3	2

* Latin square.
† I.e. four randomized blocks of sixteen plots each.

4. SAMPLING ERRORS PER CENT PER METRE

The sampling errors per cent per metre of row length for the ratio r of grain to total produce are shown in Table II. Where the samples were taken from the stooks, the average number of metres sampled was estimated from the ratio of the weight of the sample to the weight of the whole crop on the plot. The sampling errors in all cases refer to the ratios of grain to *dry* total produce, as these were the figures with which Yates & Zacopanay dealt.

Table II. *Sampling errors of the ratio of grain to total produce*

Exp.	Method of sampling	Mean yield of grain cwt. per acre	Area of plot acres	Size of sampling unit metres	Sampling error % per metre
1	R.	32·3	1/40	5·4	16·8
2	R.	29·9	1/100	1·9	10·0
3	R.	20·8	1/100	2·0	15·0
4	R.	25·1	1/40	[5·9]	[29·1]
5	{R.	14·7	1/120	{4·0	{13·8
	{G.	15·1		{3·0	{12·5
6	G.	5·6	1/40	5·6	13·7
7	{R.	33·5	1/40	{2·6	{7·0
	{G.	33·6		{3·1	{7·3
				Mean	12·6

In the first four experiments sampling errors are obtainable only for the random samples, since only one grab sample was taken per plot. In exp. 6 the random samples were unfortunately bulked for threshing.

The sampling errors per cent per metre are considerably higher than Yates & Zacopanay's figure of 7·14 %. Exp. 4 may perhaps be omitted

in reaching an average figure, since 12 % of the samples were reported as damaged by mice during storage. These samples were excluded from the statistical analysis, but five other samples also showed an anomalously low ratio of dry total produce to wet total produce, as well as an anomalously low grain/total produce ratio. These samples might perhaps be regarded as affected by damage which was not reported. The experiment was, however, one in which different leys were growing under barley and the samples in question all came from plots growing a clover-ryegrass mixture, so that they may have contained a substantial amount of the undergrowth. In any case it is clear that if there is a vigorous and variable undergrowth of ley or weeds, this method is likely to give high sampling errors.

Excluding exp. 4, the average value for the sampling error is 12·6 % per metre. There are several reasons which might account, in part at least, for the higher value obtained.

Size of plot

The criterion used, sampling error per cent per metre, is likely to increase as the size of the plot increases. While no correlation is evident in Table 11 between sampling error and size of plot, the average plot size in these experiments was considerably larger than in Yates & Zacopanay's experiments, in which most of the sampling subplots were only 1/200 acre. Since, however, Yates & Zacopanay used only a fraction of their data for this particular calculation, some additional information on the effect of plot size was obtained by calculating the sampling error of r for six of their experiments in which the plots were 1/80 acre. The results are shown in Table III.

Table III. *Sampling errors of the ratio of grain to total produce (from 1/80 acre plots)*

Exp.*	Crop	Size of sampling unit metres	Sampling error % per metre	
			r†	Grain
4	Barley	5	5·98	23·7
7	Barley	1	9·06	30·3
10	Wheat	1	8·89	28·8
10	Barley	1	10·57	32·5
11	Wheat	1	9·42	22·8
11	Barley	1	6·76	33·5
		Mean	8·45	28·6

* In Yates & Zacopanay's notation.
† The method by which these figures were obtained is discussed in the Appendix.

The average value, 8·45, is somewhat larger than the previous figure of 7·14 for smaller plots, but is still considerably below 12·6. The average

sampling error for the yields of grain in the same experiments was 28·6%, so that the relative efficiency of the two methods works out at almost the same figure as Yates & Zacopanay obtained. It does not appear as if the difference in the size of the plots can account for more than a small part of the increase from 7·1 to 12·6%.

Size and type of sampling unit

The sampling error of r will also depend to some extent on the size and shape of the sampling unit. As a rule, it is to be expected that for the same total percentage sampled, a few large sampling units will be less efficient than a larger number of small sampling units. In the present experiments the average size of the sampling unit was 3·5 m. as against 2·0 m. in Yates & Zacopanay's experiments, and this difference might partly account for the higher sampling error. In this connexion it would have been instructive to compare the variation in r between samples taken from the same sheaf with that between samples taken from different sheaves, but this is not possible from the way in which the samples were selected. It is also possible that the reaper or scythe gives a less even cut than is obtained when small samples are cut by hand from the standing crop.

Presence of weeds or undergrowth

This point has already been mentioned in discussing exp. 4 in Table 11, but it applies, to a less extent, to all experiments. In Yates & Zacopanay's experiments, the samples were cleared of weeds before determining the weights of grain and straw, whereas in sampling for the grain/total produce ratio it is essential that the sample should not be cleaned of weeds. Thus the presence of weeds, from which few experiments are entirely free, adds to the variability of r, particularly so as weeds compete with the crop and are more likely to abound in poorer patches, where the value of r is already low.

5. The correction for loss of moisture

No discussion has so far been given for the correction which must be made for the amount of moisture in the total produce as weighed on the field. Since this correction is made from the samples, it will involve some loss of information, so that the sampling errors given in the preceding section for the ratio of grain to *dry* total produce do not represent the whole of the sampling error involved in this method.

The yield of dry grain of any plot is most simply obtained by multiplying the yield of wet total produce by the ratio, in samples from that plot, of the total yield of dry grain to the total yield of wet total produce. The percentage sampling variance per plot of the yield of dry grain will be given (with all necessary accuracy) by the percentage sampling variance of the ratio of dry grain to wet total produce, divided by the number of samples taken per plot. This can be calculated if the samples were weighed individually on the field and threshed individually.

Since the sampling errors of the ratio of dry grain to dry total produce have already been discussed, it will be more convenient to discuss here the sampling errors of the ratio of dry total produce to wet total produce, assuming these ratios to be independent. In general, however, the more direct approach is preferable, since the assumption of independence is not likely always to hold.

Unfortunately, little evidence on the dry/wet ratio is obtainable from these experiments. The samples were weighed individually on the field in only three experiments, nos. 3, 4 and 7, mainly because the accuracy of the spring balance and the external conditions did not appear to justify weighing each sample. Of these experiments, no. 4 has already been noted as exceptionally variable, while in no. 7 there appears to have been a zero error in the spring balance, since almost all the dry weights of total produce were slightly higher than the wet weights.

In exp. 3, the sampling error per cent *per plot* for the ratio of dry to wet total produce was 7·03, as compared with 7·50 for the ratio r of dry grain to dry total produce. The corresponding figures in exp. 4, omitting the plots undersown with the clover-ryegrass mixture, were 7·45 and 8·50. These figures suggest that almost as much information is being lost in estimating the correction for drying as in estimating the ratio of dry grain to dry total produce. If this is true, the accuracy of the method is only half that indicated by the figures in the last section. There is, however, reason to believe that these results are not representative, since rain fell during the sampling of exp. 3, some samples being wet when weighed, and in both experiments there was an unusual amount of drying-out, the mean values of the ratio of dry to wet total produce being 0·628 and 0·673 respectively.

For the remaining experiments, the experimental error between plots for the ratio of dry to wet total produce of the samples may be used as an upper limit to the corresponding sampling error within plots. It may be mentioned that in exp. 3, the sampling variance of the dry/wet ratio

was practically equal to the experimental variance, though there were significant differences between rows, columns and treatments, while in exp. 4 the sampling variance was less than half the experimental variance. The results *per plot* for the other experiments are shown in Table IV.

Table IV. *Experimental errors per cent per plot of the ratio of dry to wet total produce*

Exp.	Mean ratio dry/wet	Experimental error % of dry/wet	Sampling error % of r
1	0·849	2·91	5·17
2	0·707	4·44	5·17
5	0·878	2·26	4·87
6	0·859	2·59	4·07

In exps. 1, 5 and 6 the percentage sampling variance of the dry/wet ratio cannot exceed about one-third of the percentage sampling variance of r, and may be substantially less. In exp. 2, in which the amount of drying was much greater, the additional loss of information was probably also greater.

If the dry/wet ratios are very variable the question arises whether the use of some average correction figure will improve matters. Clearly such an average can only be properly employed if the dry/wet ratios are unaffected by the treatments, for if they are so affected the use of an average will distort the treatment differences. Actually four of the six experiments considered showed clear differences between treatments, and exp. 3 also falls into this category if the clover-ryegrass plots are included. The use of an average correction figure is therefore inadvisable.

Such distortion can of course be avoided by using a separate correction factor for each treatment, based on the average dry/wet ratio for all replicates of that treatment. There is no point in following this course, however, since the results will be almost the same as if each plot is corrected separately. The only effect will be to give a spuriously low estimate of experimental error.

6. Comparison of grab with random samples

Direct comparison of the sampling errors of r for random and grab samples can be made in only two of the experiments in Table II, nos. 5 and 7.

In exp. 5 grab sampling was somewhat more accurate, though not significantly so, while in exp. 7 there was little to choose between the two methods.

A less direct comparison may be obtained by calculating the between-plot errors of the yields of grain given by the two methods (after elimination of treatment and block effects). Some allowance must be made for the difference in the amounts which were sampled under the two methods. In exp. 1, for example, two random samples each of about 954 g. total produce were taken, as against one grab sample of 794 g. The sampling and experimental errors per cent *per plot* for the random samples were 5·15 and 8·67 respectively. The estimated experimental error per cent, if only one random sample of 794 g. had been taken is

$$\left\{(8\cdot67)^2+\left(\frac{2\times954}{794}-1\right)(5\cdot15)^2\right\}^{\frac{1}{2}}=10\cdot8,$$

and this figure is comparable with the experimental error per cent for grab sampling. The adjustment for the size of the individual sample in the above formula is open to question, since a sample of twice the size, *taken from the same sheaf*, would probably not be twice as accurate. Since the grab samples were usually the larger, the adjustment possibly favours the random samples slightly.

Table V. *Experimental errors per cent per plot of the yields of grain*

	Method of sampling	
Exp.	Random	Grab
1	10·8	7·9
2	7·6	10·4
3	15·5	12·8
4	17·2	17·1
5	8·3	9·3
6	14·7	14·0
7	6·8	6·9
Mean	11·6	11·2

Random samples gave a smaller experimental error in two experiments, grab samples in three, while the remaining two experiments showed practically identical results. Thus grab sampling appears to be no less accurate than random sampling.

The mean yields of grain obtained by random and grab sampling are shown in Table VI. The right-hand column shows the difference between the yields from grab and random sampling as a percentage of the yield given by random sampling.

Except in exp. 4 the grab samples gave slightly higher yields of grain than the random samples. The biases are, however, in no case large.

Both random and grab sampling gave a positive bias in yields as

compared with full harvesting in exps. 1 and 3. In exp. 3 the difference is due almost entirely to a greater drying out of the total produce than of the samples.

Table VI. *Comparison of mean yields by random and grab sampling*

Grain: cwt. per acre

Exp.	Crop	Full harvesting	Random sampling	Grab sampling	% bias in grab
1	Wheat	30·59	32·36	34·33	+6·1
2	Wheat	—	29·88	31·55	+5·6
3	Wheat	18·57	20·83	21·45	+3·0
4	Barley	- -	25·07	23·95	−4·5
5	Barley	—	14·74	15·14	+2·7
6	Barley	—	5·44	5·57	+2·4
7	Oats	—	33·50	33·60	+0·3

A more detailed examination of the treatment means in these experiments shows close agreement between results from random and grab sampling.

7. Discussion of results

Owing to the uncertainty about the sampling variance of the ratio of dry to wet total produce, the total sampling error involved in sampling for the ratio of grain to total produce cannot be fixed definitely for these experiments. An average figure of 14·5% per metre of row length for the ratio of dry grain to wet total produce is probably not far wrong. (This represents an increase in the average sampling variance in Table 11 by one-third to allow for the sampling variance of the dry/wet ratio.) With this figure, a sample of 25 m. per plot gives a sampling error of 2·9% per plot. With an experimental error of 7·5% per plot, the loss of information is about 13%, i.e. an amount which could be more than offset by adding an extra replication to an experiment with between four and seven replications. This amount of sampling represents about 5% of the total produce in a 1/40 acre plot.

This figure is subject to qualification according to the conditions of the experiment. If the crop is fairly dry and free from weeds or undergrowth when it is being sampled, or if the plot size is only 1/100 acre, some reduction may perhaps be allowed in the number of metres sampled, though it would be advisable to collect more experimental data on this point.

The size of the samples taken in these experiments was probably too large. It might be better to take not more than 2 m. of row length for

each sample. It is easy to calculate, for any particular experiment, the fraction of a sheaf necessary to secure such samples. For example, in a 1/60 acre plot, sown at 7 in., there are about 380 m. of row, and if there are twenty sheaves per plot, each sample should be $\dfrac{2 \times 20}{380}$ of a sheaf, i.e. about one-tenth.

Apart from the small positive bias in the yield of grain, there appears to be no objection to grab sampling as carried out in these experiments. In practice, one might take first two random samples of about 2 m. each, and then a further eight grab samples of about the same size. The random samples would serve as a check on the others, and the whole process would require considerably less time than ten random samples.

Although this method has not proved as accurate as was anticipated, considerable time and labour still appears to be saved as compared with the previous method of random sampling from the standing crop without weighing total produce. If the figure of 28·6 % per metre (from Table III) is taken as a comparable value for the sampling error of the yield of grain by the latter method, about one-quarter of the number of samples is needed if total produce is weighed and the samples are taken from the sheaves. If most of the sampling is done by grabbing, this can be done in little more than one-eighth of the time (in exp. 5, for example, seventy-two random samples from the standing crop required 10 man-hours, including bagging and labelling, while an equal number of grab samples took 5 man-hours). As far as can be judged, the time taken to weigh the samples and total produce is not more than twice the time required to select, bag and label an equal number of grab samples. Thus the field operations require only about three-eighths of the time taken by the previous method. There is also a considerable gain in time during threshing, which is also of importance, as with the machines at present available threshing occupies a large proportion of the total time.

The new method is somewhat more exposed to weather hazards at the time of sampling. For instance, if rain falls after total produce has been weighed and while the samples are being taken, the samples which have already been drawn must be protected from the rain, while the total produce may have to be weighed again on plots which have not yet been sampled. On the other hand, it is extremely difficult to sample from the standing crop if it is badly lodged, whereas such a crop presents no special difficulty once it is in the sheaves.

SUMMARY

In a number of cereal experiments, three on wheat, three on barley and one on oats, the yields of grain and straw per plot were estimated by weighing the total produce on each plot and taking samples, usually from the sheaves, to estimate the ratio of grain to total produce. This paper discusses the sampling errors of this method. The method proved considerably less accurate than was anticipated from previous calculations made by Yates & Zacopanay. Amongst the reasons which are suggested to account for this are the larger sizes of plot and sampling unit used in these experiments and the additional variability introduced by the presence of weeds, undergrowth and moisture.

Nevertheless, the method appears to be substantially superior to the older method of cutting small areas from the standing crop, without weighing total produce, only about one-quarter of the number of samples being required to obtain results of equal precision.

The samples were taken both by an approximately random process and by grabbing a few shoots haphazardly from each of several sheaves. The grab samples gave on the whole a slightly higher yield of grain, the greatest positive bias being 6%, but were otherwise just as accurate as the random samples. Since the grab samples can be selected and bagged in about one-third of the time required for random samples, their use is recommended for the majority of the samples required in any experiment.

The validity of an approximate formula for calculating the variance of a ratio (in the present instance the ratio of grain to total produce) is discussed briefly in an appendix.

APPENDIX

The validity of an approximate formula for the variance of a ratio

To avoid the labour of calculating the actual ratios of grain to total produce, Yates & Zacopanay used an approximate formula expressing the variance of the ratio in terms of the variances and covariance of grain and total produce, most of which they had already calculated for the earlier part of their paper.

Let g, t denote the grain and total produce yields of a sample and r their ratio, and let $\bar{g}$, $\bar{t}$ and $\bar{r}$ be the corresponding means over all samples taken. Then as a first approximation

$$\frac{1}{\bar{r}^2} V(r) = \frac{1}{\bar{g}^2} V(g) + \frac{1}{\bar{t}^2} V(t) - \frac{2}{\bar{g}\bar{t}} \text{Cov.} (gt).$$

The most important condition required for this approximation to be satisfactory is that the standard errors of g and t should be small relative to their mean values, though so far as I am aware, the limits within which the formula applies have never been investigated. The standard errors of g and t were nearly all under 20 % in the experiments which Yates & Zacopanay used, but in the 1/80 acre plots given in Table III, they were sometimes as high as 30 %, so that some investigation is needed of the accuracy of the approximation under these conditions.

To proceed to a second approximation, the form of the joint distribution of g and t must be specified. If we assume that they follow the bivariate normal distribution, and write

$$c_{11} = \frac{1}{\bar{g}^2} V(g), \quad c_{12} = \frac{1}{\bar{g}\bar{t}} \text{Cov.} (gt), \quad c_{22} = \frac{1}{\bar{t}^2} V(t),$$

the second approximation is

$$\frac{1}{\bar{r}^2} V(r) = (c_{11} + c_{22} - 2c_{12}) + (6c_{22}{}^2 + c_{11}c_{22} + c_{12}{}^2 + 2c_{11}c_{12} - 10c_{12}c_{22}).$$

In the present examples, c_{11} and c_{22} are always nearly equal. If we write $\sigma^2 = \frac{1}{2}(c_{11} + c_{22})$, $\rho\sigma^2 = c_{12}$, the second approximation may be written, with sufficient accuracy,

$$\frac{1}{\bar{r}^2} V(r) = (c_{11} + c_{22} - 2c_{12}) \{1 + \frac{1}{2}(7 - \rho)\sigma^2\},$$

or, since the correlation coefficient ρ is usually near 1,

$$\frac{1}{\bar{r}^2} V(r) = (c_{11} + c_{22} - 2c_{12})(1 + 3\sigma^2).$$

This formula shows that if the standard errors of g and t are about 10 %, the first approximation underestimates by about 3 % relative to the second approximation; if the standard errors are 30 %, the first approximation underestimates by 27 %.

The errors involved in the use of the second approximation arise from (1) the assumption that c_{11}, c_{12} and c_{22} are equal to the corresponding population values. This error is unlikely to be serious in these experiments since the estimates were derived from a large number of degrees of freedom; (2) the assumption that g and t follow the bivariate normal law. It is not possible to assess the magnitude of the error from this source without further computation, although the marginal distributions of g and t tend to be slightly positively skew; (3) neglect of the higher terms in the approximation. These terms are likely to be important only when the standard errors of g and t are over 25 %.

As a check on these approximations, the actual sampling errors of grain/total produce were computed for about half the data from each plot in four of Yates & Zacopanay's experiments. These are compared with the first and second approximations in Table VII below.

Table VII. *Check on the approximate formula for the sampling variance of r*

| | | Sampling variance of r | | |
| | | First approximation | Second approximation | Actual |
Exp.*	Crop			
7	Barley	62·9	79·8	82·1
11	Wheat	44·9	51·7	45·7
11	Barley	76·5	100·1	88·8
17	Barley	18·6	20·0	22·5

* In Yates & Zacopanay's notation.

The first approximations are all less than the actual values, but the second approximations do not appear to underestimate on the whole. In exp. 11 the second approximations are rather poor, but in view of the large variation in the sampling variance of r, they are probably sufficiently close for the present purpose.

The substitution of the second for the first approximation makes little difference to Yates & Zacopanay's results, merely increasing the average standard error of r % per metre from 7·14 to 7·50. The figures given in Table III for the 1/80 acre plots are the actual values of the sampling errors of r in the exps. 11 and 17 and the second approximations in the other experiments.

REFERENCE

YATES, F. & ZACOPANAY, I. (1935). *J. agric. Sci.* **25**, 545–77.

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GROWTH AND DEVELOPMENT IN THE PIG, WITH SPECIAL REFERENCE TO CARCASS QUALITY CHARACTERS. I[1]

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(With Plates 1–5 and Eighteen Text-figures)

CONTENTS

GENERAL INTRODUCTION

RESEARCH of recent years into the many problems associated with the production of high-quality meat—whether this be beef, mutton, lamb, pork or bacon—has emphasized with increasing force the necessity for more fundamental knowledge of growth and development of the animals

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[1] It is hoped that subsequent parts will appear in future numbers of the *Journal*.

concerned before effective control of their meat qualities can be achieved by the breeder and feeder.

While workers in the general field of Animal Husbandry and the associated specialist sciences have contributed a considerable volume of essential information in respect of meat production, much difficulty is experienced in any attempt to collate this in an endeavour to enunciate general principles. There are many reasons for this. A large proportion of studies have been concerned with essentially localized and specialized problems. Work with the larger animals by reason of the nature of the material is slow, difficult, and costly, and many experiments in consequence have been governed by commercial considerations which have invariably placed severe limitations on the nature and extent of the work as well as upon its value. Concepts of what constitutes "meat quality" too, have seriously restricted the interpretation and application of many results. It is widely recognized that not only do different countries, and even different markets within any one country, vary materially in their quality requirements, but also that marked variations in consumer demand from time to time have been, and are likely to continue to be, responsible for revolutionary changes in the type of carcass required from all classes of live stock.

While this is so, it is not impossible to define "meat quality" in terms capable not only of universal application but also of providing a fundamental basis for its scientific study. Such a definition cannot embrace all the details of quality, but it can include its major aspects. Thus, the value of any meat animal in any market is dependent basically upon the proportions of the various parts of the carcass and upon its relative composition in terms of bone, muscle, fat, and offals.

We believe that these characters are the result of growth and developmental changes occurring within the body; that differences in the rate and order and extent of development of particular parts and particular tissues are responsible for the differences in the form and composition, and in consequence, in the meat quality of individual animals, of animals of different weights, of different breeds and to a large extent even of different species. We further believe that many influences capable of general description, as hereditary and environmental in origin, are actively concerned in controlling and modifying these growth and developmental changes.

In the general field of biology, Thompson[1] (1917) has stressed the

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[1] A list of references will be given at the end of the concluding part which will appear in a subsequent number of the *Journal*.

relationship between differential growth and all organic forms save the simplest. In the specialized field of animal production studies this approach owes much to the work of Hammond (1932a), who has clearly shown the dependence of conformation and composition of the sheep upon growth and developmental differences, and who has produced evidence suggestive of a similar close relationship in cattle (1929) and pigs (1932b). Huxley's (1932) quantitative formulation of heterogenic growth and demonstration of the widespread existence of growth gradients in widely divergent biological forms provides a further sound ground for a "growth approach" to the problem.

By a detailed study of growth and its relationship to environmental influences we aim, therefore, to build up that body of knowledge which is essential if we are to obtain effective control of the pig as a meat-producing animal. We are not concerned with the investigation of the suitability, or otherwise, of any particular methods in relation to any specific markets, but rather by the study of growth of the animal and its parts, and of its reactions to influences universally operative, do we hope to attain that grasp of the general principles involved that applications will result for all methods and for all markets.

EXPERIMENTAL METHODS AND MATERIAL

(1) NATURE AND SCOPE OF EXPERIMENTS

Proceeding concurrently, our investigations have fallen along two main lines.

The thesis that the form and composition of the animal body are the result of differential growth and development of these characters has emphasized the desirability of studying the changes concerned as they normally occur with age. We have been interested, therefore, first in the task of building up a composite picture in these respects, for the animal with which we are dealing—the pig. The study covers the post-natal stage only and involves a detailed anatomical examination of normal, average and uniform pigs at monthly intervals from birth to seven months of age. Growth has been interpreted in its widest sense and has involved consideration not only of live weight and body form, but also of all the constituent parts of the animal capable of measurement with the technique employed. The results of this study—as yet incomplete—are reported in Part I.

The second and major part of the work deals with the interplay of growth and environment and the resultant effects upon the animal body.

We have been concerned with examining how far it is possible to control the animal by taking advantage of the manner of its development and the possible relationship between the latter and certain major and specific environmental influences. The proposition may be stated more concretely thus: if the animal is the result of differential relationships between the growth of its constituent parts, and if these relationships are capable of environmental modification—that is, if the growth of constituent parts is not affected equally by external conditions such as nutrition and temperature—then the imposition of environmental variations throughout the growth period or over particular stages should result in differences in the form and composition of the resulting individuals.

For example, Hammond (1932a) has shown that in the sheep. muscle and fat have different rates of growth and in consequence a different order of development, muscle being earlier developing making a greater proportion of its growth early in life. The provision of favourable or unfavourable conditions for growth over particular stages should, in consequence of the growth differential between them, result in variations in the proportion which muscle bears to fat at the conclusion of the treatment. A series of experiments to test this hypothesis have been designed and are reported in Parts II and III. We have taken rate of live-weight growth as our criterion of environmental differences, since most and indeed all the major variations in external conditions are reflected in and are measurable by the growth curve of the animal, and since, further, we believe that it is through the latter that environment mainly produces those effects upon the body in which we are interested. The general plan of the experiments is illustrated in Text-fig. 1.

Using comparable animals it will be seen that the experimental procedure has been to produce marked differences in the shape of the growth curve of the animals under the respective treatments; that, in fact, treatment differences consist solely of differences in growth curves. Control of the shape of the curve is secured by quantitative control of the plane of nutrition operative from birth. Animals are reared from birth to 16 weeks on a High Plane and on a Low Plane of nutrition respectively, using qualitatively identical rations. At this stage a change in the treatment of some individuals occurs. While some of the High-Plane and some of the Low-Plane individuals continue on a High and Low Plane respectively until they attain a weight of 200 lb., the treatment of the remaining animals is reversed. The High-Plane animals are changed to a Low and the Low to a High Plane of nutrition, and their growth

controlled so that the individual pairs on each treatment reach 200 lb. at the same age.

Slaughter and detailed examination by anatomical dissection is effected at two stages; at 16 weeks when sufficient individuals on each treatment are killed to compare the effects up to the point of change over; and at 200 lb. when the animals on the four main treatments are killed. The
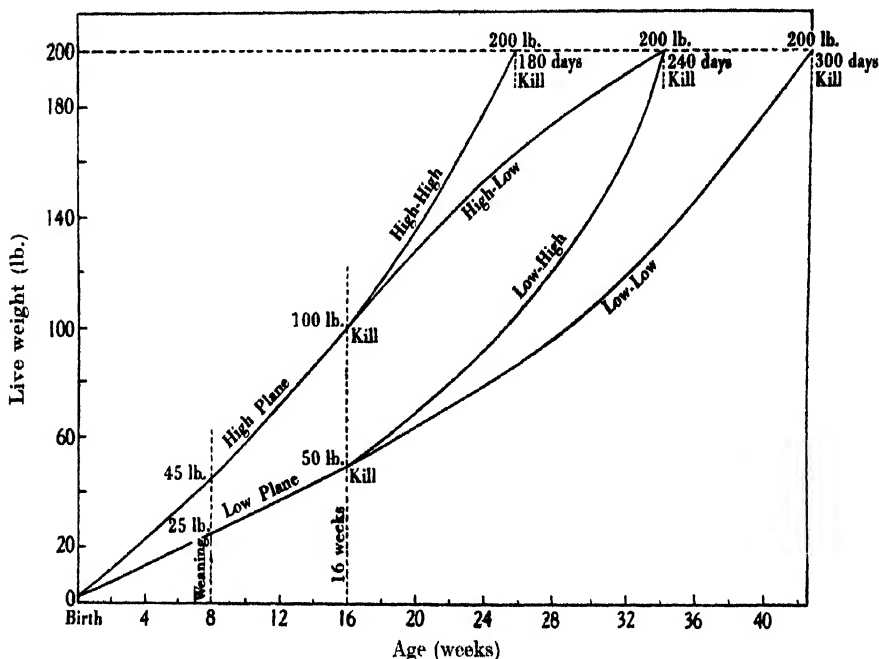
Text-fig. 1. Plan of experiment. Live-weight growth curves to be secured by quantitative control of the plane of nutrition. Differences in shape of growth curves between all treatments to be accentuated if possible.

experiment thus covers the live-weight range of commercial pig production, and the two killing stages also conform to the killing weights of porker and baconer production respectively. It will be noted that the plan permits of three main types of comparison:

(a) Pigs of the same age but of different body weight.

(b) Pigs of the same body weight but of different ages.

(c) Pigs of the same body weight and the same age, but with different shaped growth curves.

It will be realized that it will be necessary to accentuate, in certain directions, the differences in the shape of the theoretical growth curves illustrated in Text-fig. 1 if the implications of the underlying theory are to be fully exploited. Thus rather than a gradual increase in the rate of

growth of the Low-High pigs after the change-over at 16 weeks, these must be speeded up as rapidly as possible. This will tend to reduce the rate of decline in growth possible in the High-Low counterparts. Similarly, it will be desirable to attain even higher rates in the High-High and lower rates in the Low-Low than illustrated, with the maximum possible difference between all treatments at the point of change-over at 16 weeks. The growth curves of Text-fig. 1 have been drawn merely to illustrate the general theoretical plan and are based on estimates of the growth capacity of pigs to be accentuated in the directions indicated if found practicable.

At this stage, also, it might be mentioned that we believe that the four distinct types of growth curve illustrated in Text-fig. 1 represent broadly the major differences distinguishable in all classes of animal production; all four types exist to a greater or lesser degree in all countries as a result of variations in the efficiency of collective and individual husbandry, while in one or more cases they are characteristic of every country in consequence of natural variations in the food supply. While the work has thus a practical background, it must be emphasized that rather than immediate practical objectives we have aimed at determining scientific principles underlying animal growth capable subsequently of practical interpretation. We have accordingly employed more extreme differences in treatment than normally met with in the field. There has been an additional reason for this; the inherent variability of any biological material renders it extremely difficult to measure and interpret differences in effects when treatment differences are small. In a project of this magnitude where only small numbers of individuals can be used, it is doubly important to employ treatments sufficiently severe to produce significant results. By going to extremes, therefore, we have endeavoured to attain conditions normally characteristic in animal work only of laboratory physiological experiments. In the experiments as actually performed, even greater differences than illustrated in Text-fig. 1 in the shapes of the growth curves were successfully obtained.

In addition to providing experimental evidence along the lines outlined the data obtained have been employed to investigate the possibility of the use of "sample joints" and of body and carcass measurements as a means of estimating the composition of the pig in so far as its major components—bone, muscle, and fat—are concerned (Part IV). As a scientific basis to stock improvement work and as a means of assessing the effect of experimental treatments on the animal body

without the necessity for the complete destruction of the carcass, such information is of value.

Mention has been made of the inherent variability of biological material; of the genetic factors which are associated with environmental influences in modifying growth changes. In addition to the use of extreme treatments as a means of overcoming this "individuality" of the animal, we have employed throughout these investigations pigs produced from an inbred strain of the Large White Breed established for the purpose of building up a stock of "standard" pigs for use in studies of this nature by Mr John Hammond, F.R.S., of the Animal Nutrition Institute, School of Agriculture, Cambridge University.

Each of the seventy odd individuals used in this study is a direct closely inbred descendant of a full brother and sister, the original foundation stock. The latter were carefully selected from the pedigree herd of the Cambridge University Farm, on a basis of performance of related individuals as well as upon individual quality. They came from a strain that had been yielding consistently good bacon carcasses as measured by official grading standards, and that was characterized by a high degree of prolificacy, constitution and milking capacity.

Four generations of close inbreeding are represented in the animals employed and the respective lines of descent of the individuals are shown in Appendix I. It will be observed that no apparent "system" has characterized the breeding policy followed, though most of the matings are either of inbred brother-sister in each generation, or of backcross of inbred daughters of successive generations to the original foundation boar. Actually the system being followed in the development of the strain is one of individual matings; of inbreeding, of and to, particular desirable animals rather than according to any recognized mechanical plan.

It is not the purpose of this communication to discuss the results of this new departure in technique in the study of the larger animals; the use of inbreeding for the purpose of securing uniformity in experimental material has been successfully applied to the rat (Wistar Institute) and the rabbit (Hammond, Animal Nutrition Institute, Cambridge) and has ample justification on scientific grounds.

It might be observed, however, that in the many hundreds of individuals so far bred, the appearance of no undesirable recessives has been recognized. Fertility has been maintained at a high level, and no

reduction in the capacity for rapid growth has been observed. Justification for the latter statement will be met with throughout this paper. Although only a few generations are represented in the pigs used, the very satisfactory degree of uniformity so far secured can also be assessed from the results of individuals on the same treatment in our experiments.

(3) Details of the dissection technique

As previously mentioned, our results are based principally upon the form and composition of the bodies of the experimental animals. These have been studied by the application of a special dissection technique developed from that used by Hammond (1932a) for the sheep, modified in the light of experience obtained from that work and according to certain structural differences between the two species.

Five distinct stages characterized the process, and these will be briefly described.

(a) *Slaughter and dressing of carcass*

As each animal reached the requisite age or weight for slaughter, it was weighed alive at the Research Station where it had been reared, and conveyed per motor van to the laboratory. Here it was weighed again immediately prior to slaughter, and then suspended by the hindlegs from an overhead beam. Bleeding was effected in about half the cases without anaesthesia, but in the later animals after stunning with an electro-lethaler. All blood was collected in a basin, spillage being gathered with cotton-wool and weighed with the bulk. The pig was then scalded as in commercial practice for removal of hair and epidermis. Considerable care was taken in this operation, the animal being shaved with a razor after most had been taken off with scrapers. Hoofs were also taken off during this process and weighed. All hair and removed skin was collected and its weight recorded after drying by pressure in a standard way.

After dehairing the body was photographed while lying fully extended on its side, the camera being placed vertically and centrally above it. The animal was next "dressed" as in commercial practice, and the organs and other offals removed, placed in a bath and maintained at body temperature until separation and weighing of the various parts could be carried out. Any blood remaining in the carcass was collected during dressing. At this stage, too, the "fillets" (psoas muscles) were carefully dissected out with a scalpel, weighed individually and retained for chemical analysis. The kidney and leaf fat (perirenal and retro-

peritoneal) and the kidneys were similarly removed and their individual weights (right and left side) recorded.

The hot weight of the resulting dressed carcass was then obtained, and its dorsal view photographed with the body suspended by the hind-feet from a standard-sized gambrel. It was removed to the cold-storage chambers of the Low Temperature Research Station for cooling at $0°$ C. Period in storage varied according to the time required for "setting" of the carcass, the progress of associated work on the organs and offals and on any other animals being dealt with at the same time. Every effort was made to keep the time as standard as possible.

(b) *Examination of organs and other offals*

While the carcass was in cold storage, the organs and other offals were dealt with. Throughout the process these were maintained at body temperature to avoid evaporation losses by using moist hot towels as wrappings. They were carefully separated into the following parts, the order being that of removal and weighing. All weights were recorded in grams.

Neck thymus. In dressing care had to be taken to dissect this out completely with the organs along which it lies. Before weighing it was carefully cleaned of adhering blood clots.

Heart thymus. Separated from any adhering fat tissue and blood clots.

Lungs and trachea. Separated from associated external blood vessels.

Heart. Emptied of remaining blood clots, and freed from the large blood vessels at their junction with heart tissue.

Oesophagus. Detached from the trachea at its upper limit on a level with the epiglottis, and at its lower at its junction with the stomach.

Pericardium, blood vessels, etc. Including blood vessels of neck and of the thorax up to the point where they enter the abdominal cavity, all blood clots, and any fat tissue and lymphatics associated with the trachea and oesophagus.

Diaphragm. Including associated fat.

Pancreas. Cleaned from associated fat tissue.

Liver. Excluding gall bladder which was weighed separately with its contents.

Caul fat. The omentum fat surrounding the stomach.

Stomach. Weighed first full and then after being cleaned of its contents.

Small intestine. Separated from the associated mesentery. Length

recorded in centimetres prior to weighing full and after removal of contents.

Rectum. Cleaned of adhering fat and mesentery. Length measured, and weights full and empty recorded.

Penis and vesiculae seminales. Including testicles if present, or

Uterus and vagina with ovaries.

Bladder. Weighed full and empty.

Caecum. Length, and full and empty weights obtained.

Large intestine. Measured and weighed full and empty after removal of as much associated fat tissue as possible. Complete removal of the latter was found impracticable, but every effort was made to ensure uniformity.

Mesentery and fat. The mesentery containing fat from which the intestines have been pulled away, together with associated lymphatic glands.

The actual separation of the various parts was, for any one experiment, invariably carried out by the same operator, while, so far as was practicable, the cleaning of the gut contents was similarly left to one man. Standard workmanship was aimed at throughout the whole process. In addition to recording the weights and measurements mentioned, samples of the caul fat and of the mesenteric fat were collected for histological study, while the colour of the diaphragm muscle on a cut surface was measured on a standard colour scale designed for the purpose.

(c) Body and carcass measurements

Additional to the photographic method of recording body form, a large number of different measurements were obtained on the body and on the carcass. These include measurements of the carcass frequently used in evaluating carcass quality, together with others likely to be of use for this purpose and for measuring differences in body form. The position of most of the measurements is illustrated in Text-fig. 2. All measurements were obtained with the fully extended carcass lying on the table. A linen tape scaled in millimetres was used for all long measures and for circumference work; but for short measures the distance was determined with a pair of steel dividers and scaled off on a wooden millimetre scale. All measurements were taken in duplicate.

(i) *Body measurements.*

In the median line along the back the following six points were marked with a scalpel; a line flush with the anterior base of the ears;

a line flush with the posterior base of the ears; at the point vertically above the junction of the first thoracic and last cervical vertebrae;
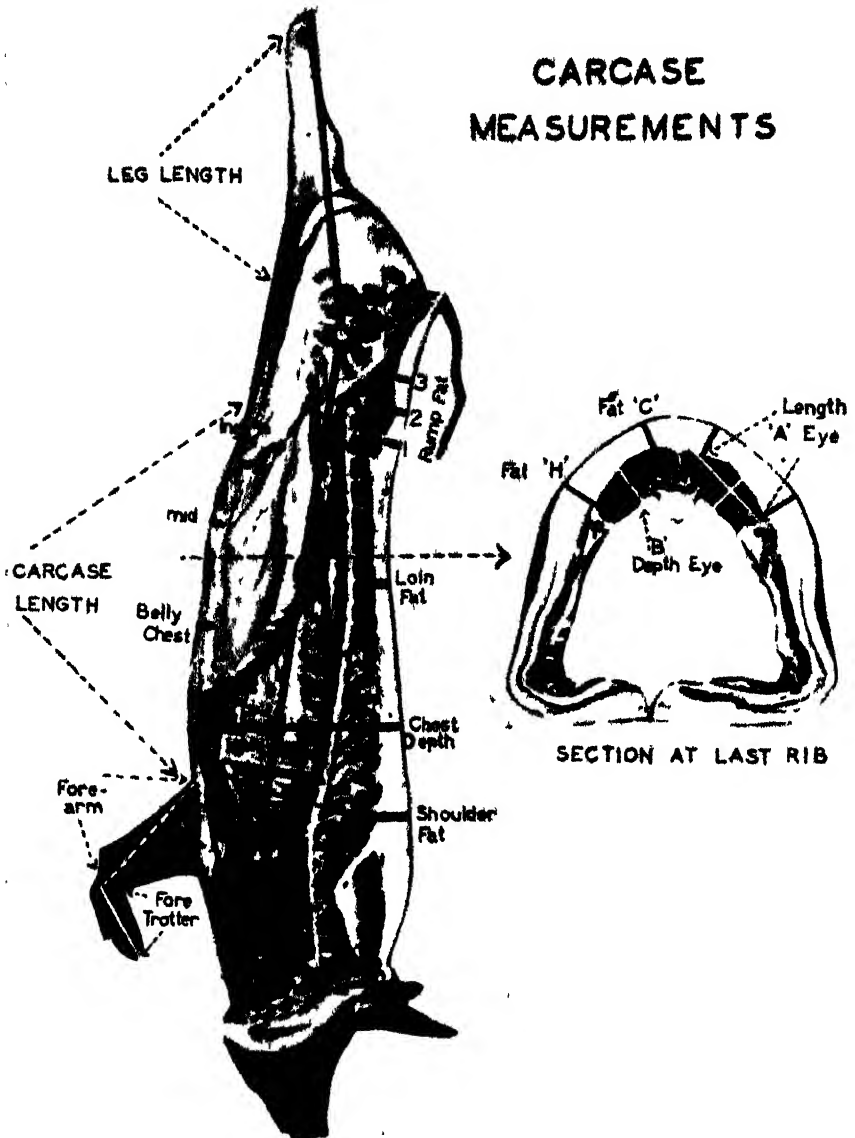
Text-fig. 2

immediately above the junction of the last thoracic and first lumbar vertebrae; at the junction of the last lumbar and first sacral vertebrae and at the base of the tail. The first and last points defined the total

body length which was measured following the curve of the body. The other points proceeding from the first backwards gave the respective lengths of *head, neck, thorax, loin* and *pelvis*.

Length of leg was measured from the lower edge of the symphysis pubis to the tip of the trotter in a straight line. Right and left legs were recorded.

The *circumference base of tail* was taken at the tail root as defined by the wrinkle in the skin at the junction.

The *chest depth* was measured using special callipers at the point of maximum depth of the thorax behind the shoulders.

Length of forearm was taken from the point of the elbow (olecranon process) to the anterior junction of the radius and carpal bones, measured on the external surface of the limb.

Length of foretrotter was taken with dividers from the carpal-cannon bone joint to the upper limit of the cleft between the toes.

(ii) *Carcass measurements.*

These are clearly illustrated in Text-fig. 2.

Carcass length from the lower edge of the symphysis pubis to the junction of the first rib and sternum. This was taken on both sides.

Streak or *belly thickness.* Measures were taken at three points on each side of the carcass. The *anterior* one hand's breadth back from the sternum and in line with and between the teats. The *inguinal* one hand's breadth from the junction of the lumbar and sacral vertebrae, and in the same line as the first. The *median* midway between these two points. Streak thicknesses were taken with a sharp steel probe and the distance scaled off as with the dividers.

Back-fat thickness. Five measurements were recorded: (1) at the thickest point in the shoulder region, (2) at the thinnest point in the vicinity of the loin-thorax junction, (3) three measures on the rump (Text-fig. 2). Since the skeleton was required intact, the carcass was not split along the backbone (as illustrated) but a strip of fat, 2 in. wide with one edge the median line, was removed along the entire length of the body. This exposed the back-fat layer, and the respective measures were then taken on the exposed surface.

(iii) *Measures on loin cut* (section, Text-fig. 2).

After taking the streak measures and prior to recording the back-fat thickness as described, the carcass was divided with the knife into two portions at the junction of the last thoracic and the first lumbar vertebrae. The cross-section was made by passing vertically down through the

belly to the posterior edge of the extremity of the last rib on each side; following then the curve of the ribs, and passing round the transverse processes of the first lumbar, and so through the joint. A photograph of the anterior surface of this section was obtained in each case and the following measurements recorded from this surface on each side:

Length of eye muscle "A"—"point to point" on the cross-section surface of the longissimus dorsi.

Depth of eye muscle "B"—the widest distance at right angles to "A" on the same muscle.

Fat at "C"—the thickness of fat from the edge of the eye muscle to, but not including, the skin at a point $1\frac{1}{2}$ in. in from the median line.

Fat at "H"—the thickness of fat from the ventral point of the eye muscle to the skin.

Thickness of skin—taken immediately above the spinous process of the vertebrae.

Colour of eye muscle—the colour taken on a special scale in daylight.

Prior to jointing, and after taking the back-fat thicknesses as described, samples were taken for histological work and for chemical analysis. For the former, the back-fat was sampled at the thickest point and thinnest point, and muscle at the eye. The complete strip of back-fat from head to tail was retained for chemical analysis, together with a strip dissected from the thorax, on the posterior edge from the back to the belly line. Samples of muscle were also obtained for the same purpose at fixed points along the back line; head, neck, thorax, loin, and pelvis. Prior to cool storage in CO_2 for this work, all chemical samples were dissected into skin, subcutaneous fat, intermuscular fat, and muscle, and the weights added to the dissection data for the respective joints involved.

(d) *Jointing of carcass*

Standardization in the method of dividing the body was a matter of considerable importance, since any lack of uniformity could result in serious errors in our studies of the relative composition of the different regions.

Two precautions were taken to minimize the dangers in this connexion. Rather than working with butchers' joints, as might seem desirable from purely commercial points of view, we have divided the carcass into well-defined anatomical regions. The main position of the division for each joint was fixed by particular skeletal joints. Further, since the cutting line through the soft parts, and away from the bones, was still subject to possible variation, the actual task of jointing was

left to the one skilled operator for any one series of pigs. The carcass had been divided into two parts during measurement. The hindquarters were first dealt with, and divided into the following joints:

Loin. A vertical cut on each side was made through the flank to the lower angle of the wing of the ilium. With the knife held vertically, the curve of the ilium wing on each side was followed, and the loin severed through the junction of the last lumbar and first sacral vertebrae.

Legs. With the carcass resting on its dorsal surface, a vertical cut was made directly over the anterior edge of the symphysis pubis and to within 2 in. (in a pig of bacon weight) of its horizontal level. The two legs were then separated in the posterior median line by a cut to the posterior edge of the symphysis ischium, laying bare the surface of the gracilis muscle on each side. The femur-acetabulum joint was then severed. Working from the symphysis ischium, the gracilis and adductor muscles were carefully separated from the ventral surface of the ischium. The ischial arch and the postero-lateral angle were then followed to the acetabular branch of the ischium, working as close to the bone as possible and severing the biceps femoris and semi-tendinosus muscles at their attachments. A vertical circular cut was then made from the acetabulum through the musculature of thigh to meet that previously made from the flank downwards. The other leg was similarly removed, the joint remaining constituting the *pelvis*.

Shoulders. These joints offered the greatest difficulty in standardizing, as there were no visible bones to act as landmarks. The pectoral muscle attaching the shoulder to the sternum was first severed, the body being laid on its dorsal surface. By traction on the lower part of the limb at first, and then with the knife, the attachments of the shoulder to the thorax were severed until the position of the scapula could be clearly defined. The knife was then drawn round the scapula, severing the latissimus dorsi muscle, and almost reaching the mid-line of the thoracic vertebrae, whence it was carried round to the base of the neck, severing the trapezius and brachiocephalicus muscles.

Head. This was severed by a vertical cut from immediately behind the base of the ears, through the atlas joint, and thence slightly forward following the natural line of the first fold of the cheek.

Neck. A vertical cut through the flesh and fat of the neck to the anterior edge of the sternum was continued through the junction of the first thoracic and last cervical vertebrae. To the dorsal surface, the line followed the anterior edge of the spinous process of the first thoracic vertebra.

The remainder of the carcass constituted the *thorax*.

Nine joints were thus obtained—head, neck, thorax, loin, pelvis, two legs and two shoulders. The weight of each in grams was ascertained immediately after separation, and prior to wrapping in cold damp towels to await dissection. Joints which could not be worked on immediately with the staff available were kept in high-humidity cool storage until required.

(e) Dissection of joints

The dissection of individual joints followed the same general plan; each was divided carefully with scalpel, forceps, and scissors into the main components, skin, subcutaneous fat, intermuscular fat, muscles, tendon and waste, glands, and bones. In addition, the head provided specialized parts and organs, and the joints of the trunk, the spinal cord. Weights of each part were recorded in grams. In each trunk joint, all muscular tissue was weighed as a whole, but in the limb joints, subdivision into muscles of the upper part of the limb, lower part of the limb, and muscle round cannon bones was made. Bones were recorded individually or in groups depending upon the joints and the nature of the bone concerned. Details in this respect can be readily obtained from the original data in Appendices II, III[1] and IV[1].

The procedure in respect to the leg joint will serve as an example of the methods used.

The joint was placed on a dissecting board covered with a damp towel. Throughout the process, the joint itself was also kept covered with a similar towel, and any handling of the meat with the fingers avoided by working through the towel itself or with forceps. The foot was removed at the metatarsal-pastern bone joint, for separate dissection. Skin and subcutaneous fat were then removed together, and any of the latter remaining on the muscle surface dissected away with scissors and added to the whole. All fat covering muscle tissue was taken as subcutaneous. Separation of skin and subcutaneous fat was effected by fixing the former to the board with drawing pins and cutting away the fat. The pre-crural glands were dissected out and weighed. Muscles grouped round the femur were next separated from those grouped round the tibia-fibula and the former removed separately from the bone. Fat lying between these was dissected away with scissors and forceps. Where such fat continued into the muscle tissue (intramuscular) dissection down to the muscle surface only was made. The resulting "thigh muscles"

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[1] These will be published in a subsequent part.

and "fat between thigh muscles" (intermuscular) were then weighed. Muscles round the tibia were similarly dealt with, giving "leg muscles" and "intermuscular fat" of leg. The same process was repeated with the muscles round the cannon except that here no separation of fat occurred.

The individual bones were next separated. Any muscle still adhering was added to the weights already obtained. The bones were cleaned of all tendon and fat down to the bone surface, and along the shafts of the long bones, of the periostium. Care was taken to leave all cartilage. Removed material, together with any ligaments, was recorded for the joint as a whole, as tendon and waste. Individual bones were weighed as they were cleaned to minimize evaporation losses. The foot was similarly treated, yielding skin, tendon and waste, and the weights of the respective pairs of bones. During cleaning, all bones were held through the damp towel. During the dissection of the leg, samples of the rectus femoris and gastrocnemius muscles and of intermuscular fat (from base of rectus femoris) were taken and preserved for histological work. The dissection results of the right and left limbs provided a useful check during the progress of the work, on the accuracy of same: the close agreement can be assessed from the raw data of Appendix IV.[1]

Apart from precision in dissection, the reduction to a minimum of evaporation losses had to be borne constantly in mind. A certain loss was found unavoidable, but the execution of the work in the humid atmosphere provided by damp towels, the avoidance of any but essential handling of parts with the fingers, the distribution of suitable parts of each joint between skilled workers as an aid to rapid completion of each together with the storage of joints not being worked on in high-humidity low-temperature chambers, resulted in extremely satisfactory results. The average loss in the dissection of a pig of 150 lb. carcass weight was of the order of 1-2 %. A big factor here, in addition to those mentioned, was the fact that each animal was worked on continuously from slaughter until the completion of the dissection. This required approximately 150 man-hours per pig. With the trained staff available and with the assistance of many interested casual workers to whom our thanks are due, no animal required longer than $2\frac{1}{2}$ days and the majority were completed in 1-2 days.

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[1] This will be published in a subsequent part.

PART I. AGE CHANGES IN GROWTH AND DEVELOPMENT

(1) INTRODUCTION—METHODS, MATERIAL

In 1935 Mr John Hammond, F.R.S., of this laboratory, commenced a comprehensive study of age changes in the growth and development of the pig. This project had for its major aim the detailed analysis and interpretation of such changes and their bearing upon problems of animal husbandry. While a considerable volume of data had been accumulated, the work was still far from complete when it was temporarily suspended in the latter part of 1936 to release pigs for the experiments described in Parts II, III and IV, and facilities for which had become available.

The present communication can therefore be regarded merely in the light of a preliminary report; incomplete not only in respect to the data but also in the aspects covered and methods of analysis used. Justification for the use of the material at all at this stage rests on the fact that sufficient is available to obtain at least a general picture of the major changes and trends involved, and that such a picture is suggestive, and in many respects definitely helpful, in interpreting some aspects of the experimental studies with which we are mainly concerned. The writer is, therefore, very much indebted to Mr Hammond for his ready permission to use the data as a basis for the present report.

We have been interested principally in establishing the general order of development in post-natal life of the various parts and tissues of the body; in separating these, out into relatively "early" and "late" developing categories. By an early-developing part we mean one which relative to another makes a greater proportion of its growth early in life. We have attempted to do this by the growth of each part relative to its size or mass at birth, using the method employed for a similar purpose by Hammond (1932a) in his study of the sheep. The size or mass of the whole or part at each age is expressed as a percentage of the size or mass of the same part at birth.

Though subject to certain disadvantages—such as involving the possibility of considerable error should the birth data be inaccurate—it throws into sharp relief the relative order of development, and provides a useful comparative measure of rates of growth in terms of the rate at which each part increases its birth size or mass, as the case may be. Limitations of the data preclude any detailed analysis by biometric methods commonly employed by those interested in the theoretical

aspects of growth, but for the major tissues—skeleton, muscle and fat—the percentage rate of growth with age has been investigated. In some cases also the relative rates of growth in terms of grams increase per week have been determined.

The raw data of the series are set out in Appendix 11. Those presented in the text are based on the mean weights and measurements of the pigs at each point.

The series is one of males, killed at monthly intervals (4 weeks) from birth to 7 months. They have been selected from those available on a basis of age for weight, so that a series typical of pigs of the Large White breed under ordinary farm conditions in Great Britain would result. That is, the growth curve constructed from their mean weights at slaughter is, for the age period covered, fairly representative of good commercial performance (Duckham, 1930). Further, the individual growth curves of the animals from birth to slaughter show no irregularities. Any individuals deviating markedly from the "normal" have been discarded. Females have not been included in any of the quantitative comparisons. They were available only with irregular frequency at the various points, and since—as will be shown later—their proportions and composition differ markedly from males it was considered advisable to confine the study to the latter at the present stage. Entire males only are involved, up to, and including, the 4-months stage; after this, castrates are included. No data are available at the 12-week stage, and only one animal at 8 and 28 weeks respectively. Three are involved at the 24-week point and two at every other age.

All pigs were from the inbred strain previously described (Details, Appendix I). They were reared under comparable conditions, feeding and management being along the lines of good commercial practice. The rations consisted of a typical commercial mixture of cereal concentrates—barley meal, flaked maize, and middlings—with fish meal as the protein supplement.

(2) RELATIVE GROWTH AND DEVELOPMENT IN BODY PROPORTIONS

Changes in body form with age are shown in Pl. 1, fig. 1. Here, in order to differentiate between changes in proportions and changes in size, all the animals have been reduced to the same height at the shoulders as measured from the tip of the trotter.

At birth the pig is largely head, neck, and legs, with a short, shallow body and poorly developed hindquarters. As it grows up, the initially

most marked change is an increase in proportional length—4 and 8 weeks—followed by an increasing tendency towards a deepening and thickening of the body. With this increased length and depth of body, the head, neck, and legs become proportionally smaller. By 24 and 28 weeks, the hindquarters have deepened and thickened so that both actually and proportionally they exceed the size of the head and neck.

Similar photographic comparisons have been made by Hammond (1927, 1932b) using pigs at more widely separated age intervals from the foetal stage to maturity. The same worker (1932a) has shown that comparable changes in body form occur in the sheep, while Brody & Ragsdale (1924) have produced similar figures for dairy cattle. While species differences are apparent—the limbs of the cow and the sheep showing proportionally greater development at birth than the pig, and the neck of the cow showing a relatively greater increase with age—the general trend is essentially similar in all three, and consists of an anterior-posterior directional development in all three dimensions—length, depth, and breadth in that order, with the limbs behaving as relative early developing parts.

Changes in proportions have also been studied by comparing the weights of the different anatomical joints as removed for dissection (Table 1). The growth in empty live weight (live weight at slaughter less contents of alimentary tract and bladder) and the growth in dressed carcass weight are also shown. From the figures showing the proportional growth of each part relative to its birth weight, it will be observed that growth in weight of the different parts confirms the pictorial representa-

Table 1. *Age changes in body proportions*

Age weeks	Empty live weight	Dressed carcass weight	Head	Neck	Shoulders	Thorax	Loin	Pelvis	Legs
				Mean weight of joint (g.)					
Birth	1337	989	225	72	226	170	59	54	183
4	5931	4413	655	364	892	1010	380	214	900
8	13209	10176	1597	691	2143	2356	775	469	2145
16	36102	27493	3219	2006	5265	6361	3158	1931	5554
20	52060	40268	3630	3672	7080	10060	3952	3568	8308
24	71442	56345	4655	4954	9886	15087	5613	5106	11045
28	100000	80469	6380	6050	13220	22639	10939	6461	14780
		Relative growth as percentage weight of part at birth							
Birth	100	100	100	100	100	100	100	100	100
4	444	446	291	506	394	594	644	396	492
8	988	1030	710	960	948	1386	1313	868	1172
16	2700	2780	1431	2786	2330	3741	5353	3575	3034
20	3894	4071	1613	5100	3132	5918	6698	6607	4540
24	5343	5697	2069	6880	4374	8875	9513	9455	6036
28	7479	8136	2836	8402	5849	13317	18541	11964	8077

tion shown in Pl. 1, fig. 1. Whereas the head and neck have increased their birth weight by 28·3 and 84·0 times respectively by 28 weeks, the loin and pelvis show an increase of 185·4 and 119·6 times at the same age. The thorax occupies an intermediate position between the neck and loin, with an increase of 133·2 times its birth weight. Note that the loin region is shown up as the latest developing part; this will be found to be substantially the case in composition as well as in gross weight.

The limbs occupy intermediate positions, the relative increase with age confirming their early developing character. The hindlimb appears slightly later developing than the forelimb.

These relationships are also supported by the consistent relative increases at each age.

It will be noted in respect to empty live weight and dressed carcass that the latter would appear to be the later developing character. Relative increase in carcass weight is greater at all ages, the difference becoming accentuated as the animal gets older. This is due to the early developing character of the body organs, and consistent with the widely known fact that the percentage dressing loss in all animals decreases with increasing weight and age. Relative growth of the individual organs is shown in a later section.

Growth in body proportions in the pig thus appear to conform in general to the "law of developmental direction" (Jackson, 1914), which with certain exceptions and limitations has been shown to apply to the growth and development of many vertebrates (Robbins et al., 1928; Huxley, 1932). We must now examine the growth of the constituent tissues and organs of the body and see whether these too follow a similar trend and to determine their manner of growth relative to the body as a whole and to each other.

(3) Proportional changes in composition of carcass
(skeleton, muscle, skin and fat)

Changes in live and carcass weight provide but relatively crude measures of growth, since the body as a whole is composed of many different tissues which may, or may not, grow in the same manner. Since the major of these are of special significance in the meat-producing animal, it is doubly important to know something about their relative growth.

Changes in bone, muscle, skin and fat are shown in Tables 2 and 3 and in Text-figs. 3–6. The composition of the carcass changes markedly

Table 2. *Age changes in composition of carcass*

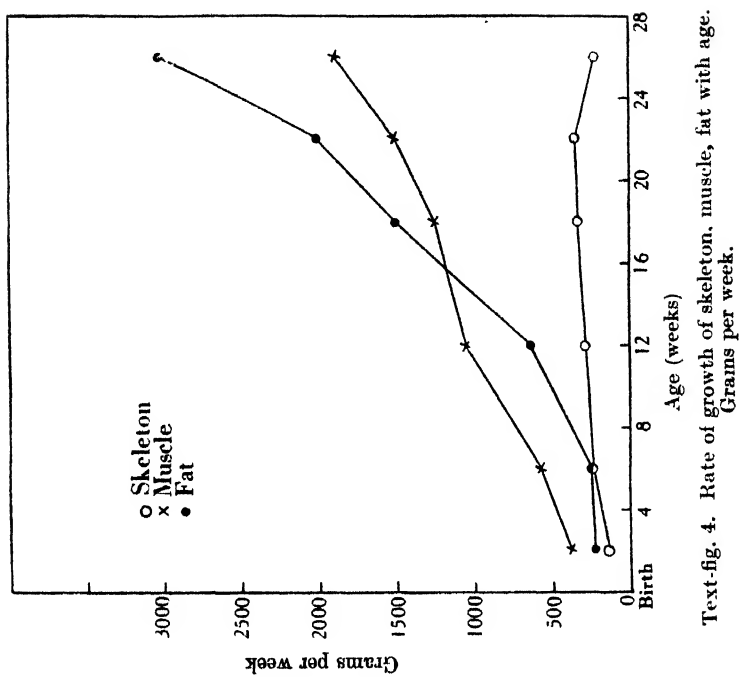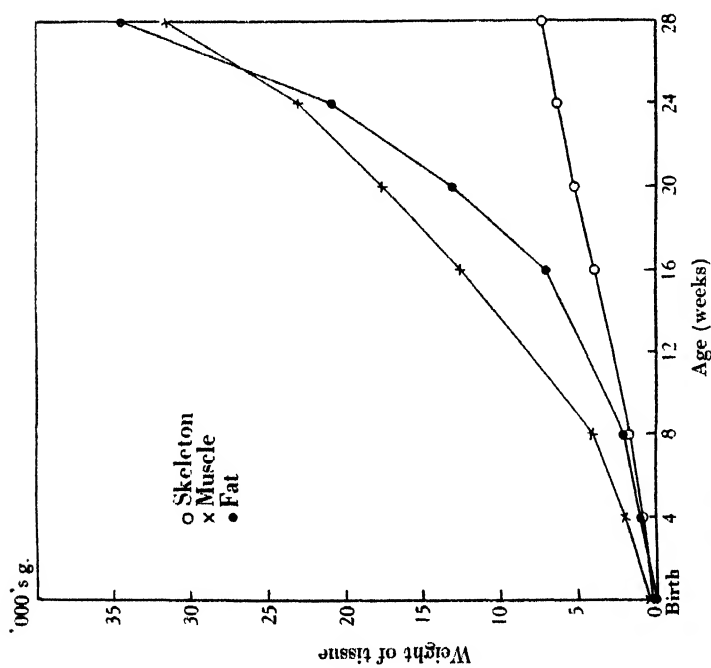|	Birth	4 weeks	8 weeks	16 weeks	20 weeks	24 weeks	28 weeks
			Mean weights (g.)				
Skeleton	242·7	767	1730	3962	5214	6438	7396
Muscle	388	1901	4182	12669	17718	23015	31647
Fat	51	984	1974	7127	13186	20889	34513
Skin	106	355	834	1738	2294	3075	3442
		Relative growth as percentage mass of tissue at birth					
Skeleton	100	316	713	1632	2148	2652	3047
Muscle	100	490	1078	3265	4566	5932	8156
Fat	100	1929	3870	13975	25854	40958	67672
Skin	100	335	787	1639	2164	2900	3247

Table 3. *Age changes in composition of carcass.*
Rate of growth in grams per week

|	Birth–4 weeks	4–8 weeks	8–16 weeks	16–20 weeks	20–24 weeks	24-28 weeks
Skeleton	131	241	279	313	350	213
Muscle	381	570	1061	1262	1513	1918
Fat	233	247	644	1515	2008	3028
Skin	62	120	113	139	223	82

with increase in age. In terms of actual weights of the respective tissues, muscle exceeds all others from birth to 24 weeks, when it is overtaken by fat. At birth, the amount of skeleton exceeds the amount of fat, but this position is quickly adjusted and the amount of bone falls below both muscle and fat from 4 weeks onwards. Skin is the tissue present in smallest amount at all ages except at birth, when it also exceeds the fat. Text-fig. 3 shows the composition of the carcass at each age.

Decrease in the percentage of bone with age in the pig has been shown to occur by Tschwinsky (1884) and Wellman (1924). Ellis & Hankins (1925) and Mitchell & Hamilton (1929) have in addition demonstrated the decrease in the percentage of muscle (protein) and the increase in fat chemically determined.

The relative order of development is clearly shown in Text-fig. 5. The skeleton increases over the amount present at birth by only 30·4 times at 28 weeks, while muscle increases its birth weight 81·6 times, and fat 676·7 times. The curve for skin follows closely that of the skeleton, and the tissue increases only 32·5 times. Both bone and muscle are thus earlier developing than fat, with bone earlier than muscle. The reason for these differences must lie obviously in differential growth rates. The rate of growth in grams per day are shown in Table 3 and in graphic form in Text-fig. 4. Bone shows the lowest rate of increase, with but a small rise to the 20–24 weeks stage, followed by a drop. Muscle has the

Text-fig. 4. Rate of growth of skeleton, muscle, fat with age. Grams per week.

Text-fig. 3. Composition of carcass with age. Skeleton, muscle, fat.

greatest rate until about 16 weeks when it is overtaken by fat, the rate of growth of which has been increasing more rapidly. Fat maintains this higher relative rate, with the result that at 24–28 weeks, about 50 % more fat than muscle is being laid down in the body.
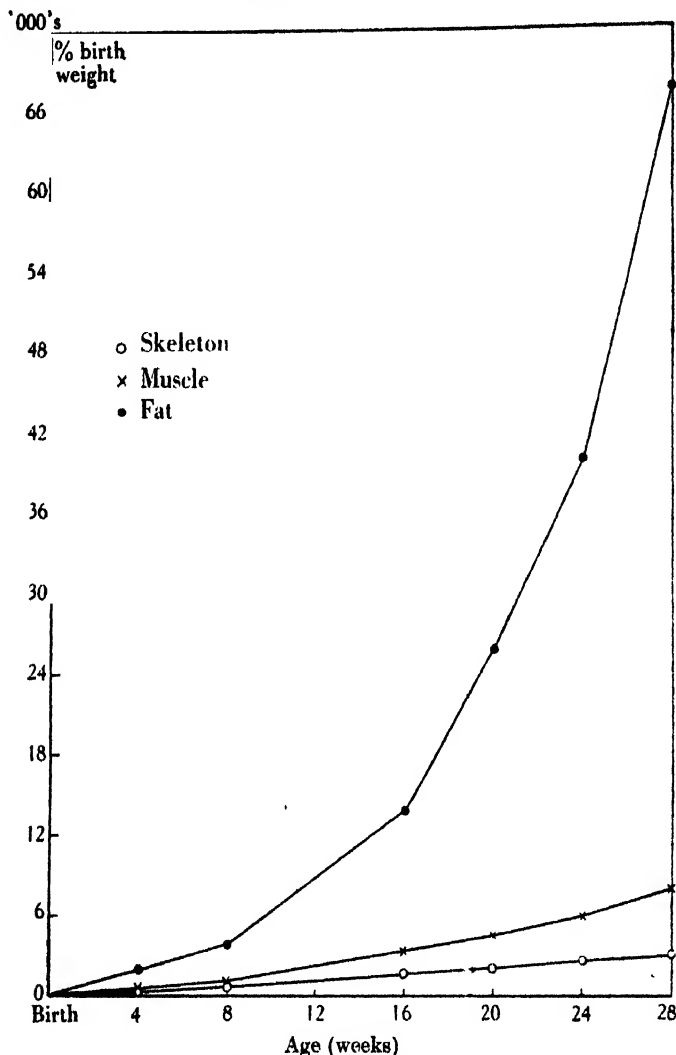
Text-fig. 5. Age changes in carcass composition. Skeleton, muscle, fat as per cent mass of tissue at birth.

These trends in order and rate agree closely with those obtained by Hammond (1932*a*) for the sheep. Relative rates of growth for the three tissues are also shown in Text-fig. 6. These confirm the trends noted. They have been calculated from the formula of Glaser (1938),

$$\log w = k \log (2t+1) + C,$$

with t including embryonic time. Glaser claims this formula, based on the "compound interest" concept of growth but modified to embrace "time from which growth is inseparable", provides a better fit with available growth data than other empirical methods so far employed. He gives numerous examples supporting his contentions.
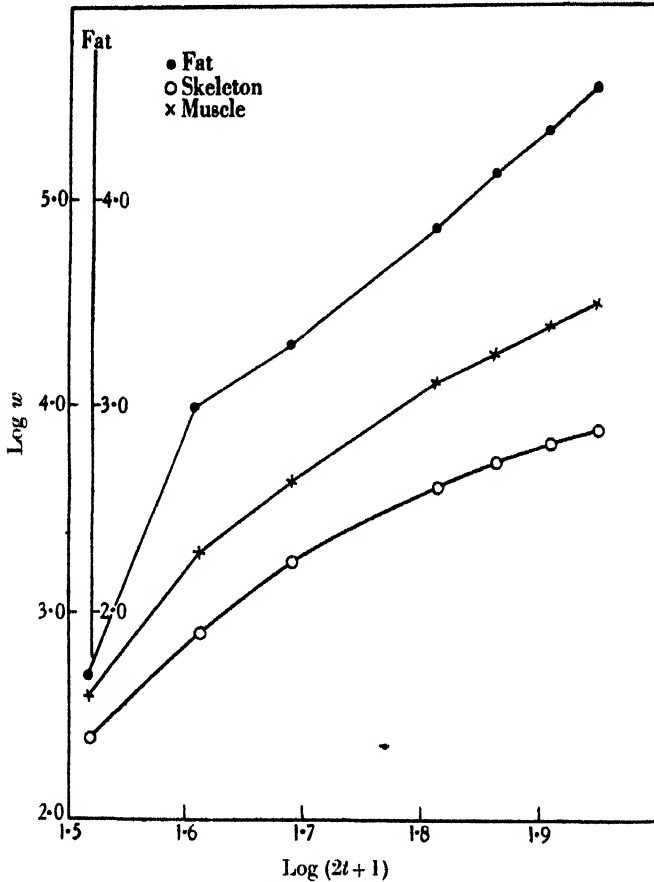
Text-fig. 6. Rate of growth of bone, muscle and fat.

It will be noted, however, that while the rate of growth is lowest in bone and highest in fat at all stages, the points by no means fall along straight lines. On the contrary, those for bone exhibit a progressive decline in rate at each age. There is an approximation of a constant rate in the case of muscle from 4 to 16 and from 16 to 28 weeks respectively and in fat from 16 weeks onwards, and it is easy to suggest that we are dealing with "stanzas" of growth, the precise limits of which could be defined with more data. It would be more difficult to justify such an assumption except on the basis of convenience. The difficulty is typical

of those met with in the application of the many formulae devised for the study of growth from theoretical points of view. It is obviously not worth while to attempt to give a value to k, so that with the data available further exploration along these lines is hardly likely to be profitable. For the same reason, and since we will later show that the different parts of the body are not affected equally by external conditions, we have not proceeded with Huxley's (1932) approach to heterogenic growth.

At the same time, Text-fig. 6 is extremely useful in demonstrating the differential rates of growth of the three tissues in terms related to the mass of the part at each age. The extremely rapid acceleration in the rate of growth of fat from birth to 4 weeks is interesting in relation to its marked fall after this age. The accuracy of this observation is dependent very largely on the accuracy of the dissection of fat in the new-born pig. At this stage, fat is extremely difficult to separate with precision. However, the data have been checked from that on four other animals not included in this analysis, while in addition it has been calculated that an error as large as 400 % in the amount present would still allow this rapid increase. Such an error is, of course, fantastic; it would give the birth pig a percentage composition in fat equivalent to a 16 week animal. The fact of a rapid initial rate, therefore, can safely be considered established, and it is interesting to speculate as to the possible reasons. Fat has undoubtedly a temperature regulating as well as a nutrient storage function, and in post-natal life temperature regulation becomes an immediate responsibility to the individual organism.

At birth the pig is but poorly equipped for this purpose so far as its subcutaneous fat layer is concerned, but the position is rapidly corrected by an extremely high rate of fat deposition. It is a matter of common knowledge that the new-born pig almost within a few days loses its emaciated appearance and assumes a characteristic rotundity of form. This "bloom" or "baby-flesh", to use terms commonly employed by the breeder, is shortly lost as rapid growth in linear proportions proceeds, to appear again only as the animal approaches the marketing stage.

To the meat producer the outstanding facts arising from this analysis are the early-developing character of bone and muscle and the late-developing character of fat. At 16–20 weeks most of the bone and nearly all the muscle of the bacon pig have developed; increase in weight after this point consists largely of fat under average conditions. The implications of this situation have already been referred to, and it is with these with which we will later be very much concerned.

(4) Relative growth and development of the organs

Here we include parts not strictly organs but removed with the latter as offals in dressing. Mean weights (Table 4) are given. Three main groupings are made; thoracic, alimentary tract, and abdominal, less tract. Note that over the later ages, the thoracic organs account for approximately 10 % of the gross weight of all organs, the tract for roughly 30 %, and the other abdominal for most of the remainder.

Table 4. *Age changes in body organs. Mean weights (g.)*

	Birth	4 weeks	8 weeks	16 weeks	20 weeks	24 weeks	28 weeks
Blood	132	384	700	2015	2749	3677	3296
Hoofs	2·9	7·1	17	41	51	71	96
Neck thymus	1·8	13·6	30	38	65	109	84
Heart thymus	1·8	5·5	10	29	40	44	61
Heart	10·2	48·5	62	165	199	254	266
Pericardium, blood vessels, etc.	2·6	11·4	20	83	114	173	181
Diaphragm	6·5	24·3	53	166	236	344	408
Lungs and trachea	25·8	88·3	193	446	553	627	778
Total thorax	45	172	328	860	1100	1430	1633
Oesophagus	1·6	4·6	15	29	40	54	61
Stomach	5·9	39	138	370	449	598	574
Small intestine	21·7	219	313	1009	1292	1579	1397
Caecum	0·9	5·3	14	76	113	123	129
Large intestine and rectum	7·5	40	189	618	879	897	1021
Total alimentary tract	37·5	303	669	1100	2774	3252	3182
Caul	0·15	1·75	3·0	34	64	101	252
Mesentery	7·25	37·5	107	367	594	822	1705
Liver	46·4	190	435	1017	1398	2098	1745
Gall bladder	0·35	1·85	12	16	27·5	36	43
Spleen	1·4	9·2	21	37	60	77	99
Pancreas	1·55	14·7	31	94	129	110	140
Kidneys	10·8	40·9	76	170	212	222	225
Leaf and kidney fat	1·4	20·7	50	238	520	1004	2295
Bladder	2·6	3·0	10	17	24	41	50
Total abdominal organs	109	622	1414	4085	5800	7769	9736
Total offals*	271	1307	2623	7652	10498	13719	15837

* Including other organs and parts removed in dressing (see Appendix II).

Relative growth of these groups and of the individual organs are set out in Table 5 and in Text-figs. 7 and 8. It will be observed (Text-fig. 7) that the abdominal organs are later developing than the thoracic. increasing their birth weight by 89·3 times as against 36·2 times. The rate of increase of the former is even greater than that of the carcass. This is due to the inclusion in the abdominal group of relatively much later developing parts (Text-fig. 8a), such as the mesentery, the kidney and

Table 5. *Relative growth of organs. As percentage of mass of organ at birth*

	Birth	4 weeks	8 weeks	16 weeks	20 weeks	24 weeks	28 weeks
Blood	100	290	530	1526	2082	2785	2495
Hoofs	100	245	586	1413	1759	2448	3310
Neck thymus	100	756	1667	2111	3611	6055	4667
Heart thymus	100	306	556	1611	2222	2444	3389
Heart	100	478	610	1626	1960	2502	2620
Pericardium, blood vessels, etc.	100	447	784	3254	4471	6784	7098
Diaphragm	100	374	815	2553	3630	5292	6277
Lungs and trachea	100	342	748	1729	2143	2430	3015
Total thoracic organs	100	383	729	1911	2444	3178	3628
Oesophagus	100	288	938	1781	2500	3375	3812
Stomach	100	661	2339	6271	7610	10136	9728
Small intestine	100	1009	1442	4649	5953	7276	6428
Caecum	100	589	1556	8444	12556	13667	14333
Large intestine and rectum	100	533	2520	8240	11720	11960	13613
Total alimentary tract	100	808	1784	2933	7397	8672	8485
Caul	100	1167	2000	22666	42667	67333	168000
Mesentery	100	517	1476	5062	8193	11337	23517
Liver	100	409	931	2191	3012	4521	3760
Spleen	100	656	1500	2642	4250	5500	7071
Pancreas	100	919	1938	5875	8322	6875	8750
Kidneys	100	373	691	1556	1927	2020	2045
Leaf and kidney fat	100	1478	3571	17000	38518	74370	170000
Bladder	100	113	385	654	923	1576	1923
Total abdominal organs	100	570	1297	3747	5321	7250	8932
Total offals*	100	482	968	2823	3873	5112	5844

* Including other organs and parts removed in dressing (see Appendix 11).

leaf fat, and the caul, which together account for a considerable proportion of the total. The relationship between all offals and carcass weight can be obtained from the total figures of Table 5 and those for the carcass in Table 1. The latter increases its birth mass 81·4 times and the former only 58·4 times at 28 weeks. The curve for blood falls below that for the early-developing thoracic group with the relatively small increase of 25 times its birth quantity. Skin and hoofs similarly appear as early developing parts. The relationships of the thymus are of interest in view of the association believed to exist between this gland and growth. The neck thymus shows a rapid increase after birth and remains relatively large throughout the most active period in live-weight gain. The heart thymus maintains a more steady rate of increase on a lower level. The thymus thus appears as a relatively early-developing organ; its maintenance of a large size during the self-accelerating phase of growth is in line with results from other animals (Anderson, 1932). Of the thoracic
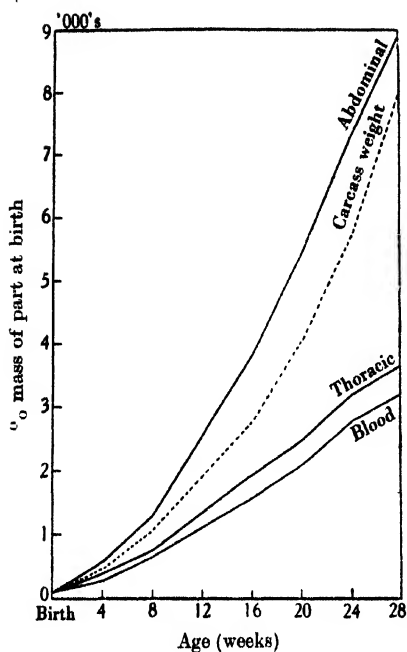
Text-fig. 7. Growth of carcass, blood, thoracic and abdominal organs.
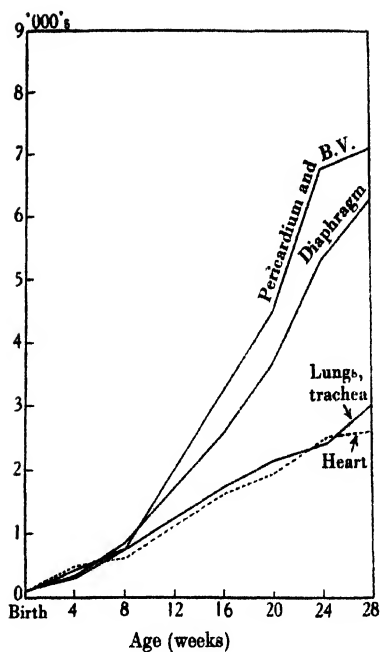
Text-fig. 7 a. Growth of thoracic organs with age.
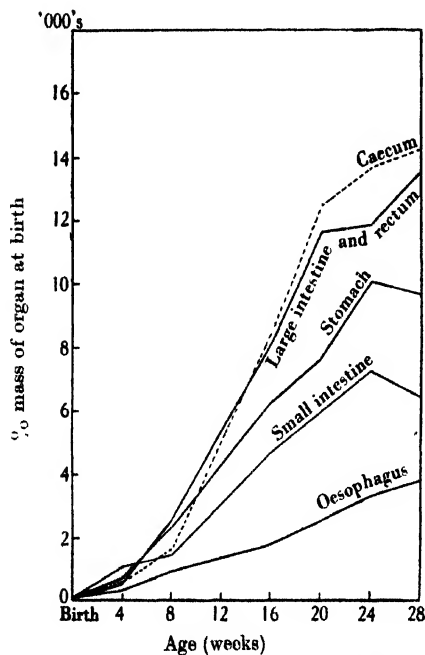
Text-fig. 8. Growth of alimentary tract with age.

Text-fig. 8 a. Growth of abdominal organs with age.

group the curves for heart and lungs follow a similar trend and level, with diaphragm and pericardium and blood vessels showing a greater increase (Text-fig. 7a). The growth of the latter two is influenced to some extent by the associated fat, the amount of which becomes relati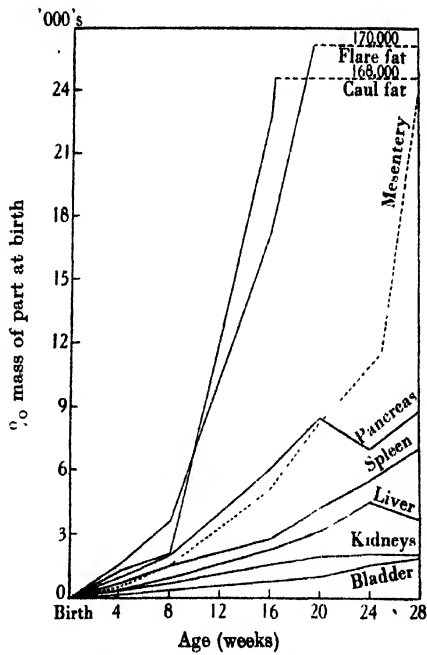vely greater as age increases. The similarity in the curves for heart and blood might be noted, while the relative early development of the former is to be expected in view of its early embryonic differentiation (Lowry, 1911).

Of the alimentary tract, the oesophagus, small intestine, large intestine and rectum, and the caecum develop in that order (Text-fig. 8). Hammond (1932a) obtained a similar order in the sheep. We do not record, however, any decrease in the weight of the small intestine with age so that, as mentioned by him, his data in this connexion may have been influenced by the method of treatment. Our curve for the large intestine and rectum is undoubtedly influenced by the increasing association of fat with age in these parts, and which it is impossible to remove completely.

Of the other abdominal organs (Text-fig. 8a) the kidneys and bladder follow a similar curve and increase relatively little with age, about 20·0 times their birth weight. The pancreas increases about the same rate as the digestive organs with which it is functionally related. The spleen follows it closely on a slightly lower level. The liver occupies an intermediate position between these and the kidneys.

By far the most striking increases are made by the mesentery which contains a large proportion of fat, the omentum, which is largely fat, and the kidney and flare fat. With increases of 235, 1680 and 1700 times their respective birth weights, their growth is in line with that for carcass fat which has been shown to be the latest developing carcass tissue. Note, however, that the relative increase in these parts, which may be collectively described as "internal fats", is well below that of carcass fat. The rate of increase of the mesentery is, as a fat-containing part, relatively lower than that of the caul and kidney and flare, because of its lower fat content consequent upon its higher proportion of connective tissue and blood vessels, and the presence of a considerable weight of lymphatic glands.

From the foregoing we obtain a picture of the organs, as parts essential to life processes and body functions, appearing relatively well developed at birth, and making smaller proportional growth in post-natal life as compared with the body as a whole. Within these, those organs associated more intimately with growth functions show greater pro-

portional development from birth. Those again whose functions are
largely or primarily those of storage of nutrient reserves, develop little
until the later stages of growth.

Table 6. *Relative growth of skull and organs of head*

Age weeks	Mean weight (g.)				As percentage of weight of organ at birth			
	Brain	Eyes	Ears	Skull	Brain	Eyes	Ears	Skull
Birth	36·3	4·0	12	59	100	100	100	100
4	50·4	5·4	58	116	139	135	483	197
8	74	7·0	110	287	203	175	917	486
16	101	10	211	514	275	250	1758	871
20	105	11	276	688	289	275	2300	1166
24	100	11	316	889	275	275	2633	1507
28	108	12	277	876	297	300	2308	1484

The relative differences between the first two types are even more
strikingly apparent if we compare with them the growth of the brain
and eyes (Table 6). These are shown in graphical form in Text-fig. 9
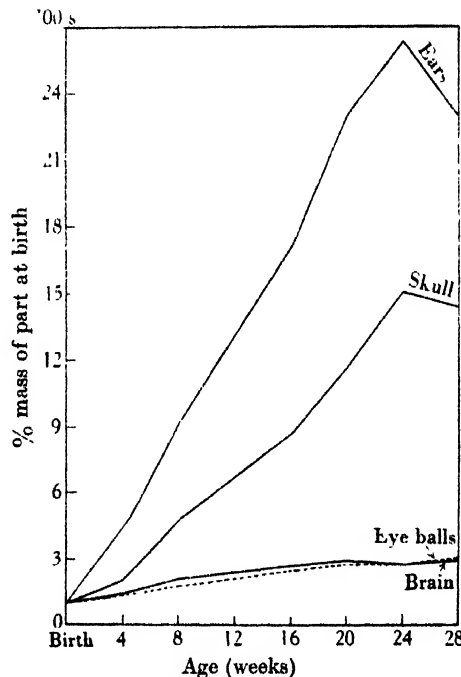
Text-fig. 9. Growth of organs of head with age.

along with the curves for the ears and the skull—one of the earliest
developing bones. The curves for eye-balls and brain are closely associated,
and each increases its birth weight only three times over the age period

Table 7. Age changes in skeletal growth.

Age weeks	Skull	Lower jaw	Vertebrae				Ribs and sternum	Pelvis	Forelimb		Hindlimb	
			Cervical	Thoracic	Lumbar	Sacral			Below cannon	Above cannon	Below cannon	Above cannon
Mean weights (g.)												
Birth	59	14·5	10·2	20·2	10·4	2·7	26·1	8·35	4·1	42·6	4·2	39·4
4	116	34	33·4	75·4	36·5	9·1	98·5	34·9	14·1	145	13·3	153
8	287	87	76	157	96	37	219	82	29·0	313	26	311
16	514	176	185	365	251	66	475	220	73	772	65	786
20	688	219	255	522	325	89	632	308	93	989	93	977
24	889	307	281	625	372	114	823	368	109	1219	104	1193
28	876	297	372	726	430	155	1005	440	132	1454	122	1351
Relative growth shown as percentage of weight of part at birth												
Birth	100	100	100	100	100	100	100	100	100	100	100	100
4	197	235	329	374	353	337	377	418	344	340	320	398
8	486	602	749	779	928	1370	839	982	707	735	627	790
16	871	1218	1823	1811	2426	2444	1820	2635	1780	1812	1566	1997
20	1166	1516	2572	2591	3140	3296	2421	3689	2268	2322	2240	2482
24	1507	2125	2768	3102	3594	4222	3153	4407	2658	2861	2515	3020
28	1484	2055	2665	3602	4154	5740	3851	5270	3220	3413	2940	3433

covered. These two must be rated as extremely early developing organs, making but slight post-natal growth.

Throughout the whole, some indication of a directional order in development may be described, but, as suggested above, a functional basis would appear to be the most important factor involved.

(5) SKELETAL GROWTH AND THE RELATIVE GROWTH OF ITS DIFFERENT PARTS

We have shown that relative to other tissues, bone, as a whole, grows at a different rate and in consequence is earlier developing. The question which now concerns us is the interrelationship of the different parts of the skeleton in respect to their manner of growth.
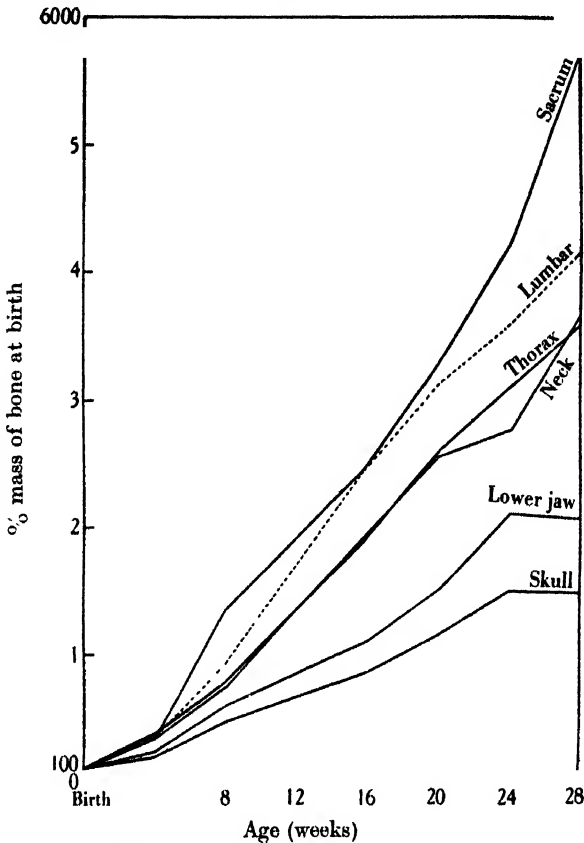
Text-fig. 10. Growth of bones of head and vertebral column with age.

That different intensities of growth exist between the different parts of the skeleton has been demonstrated by many workers (Hammond, 1932*a*), and the relationship of this situation to the conformation and

productive capacity of our domestic animals has been the subject of much study, though little systematic work has been done upon the pig. The age changes in the fresh weight of the major anatomical bone groups are shown in Table 7.

In respect to the bones of the head and vertebral column, it is clear that the skull and the lower jaw both make a relative smaller amount of growth after birth than do the vertebrae. The lower jaw increases its birth weight slightly more than does the skull (Text-fig. 10). Similarly, within the vertebral column, differences exist. These indicate a graded effect as one proceeds from neck to sacrum, with the lumbar and sacral groups showing relatively greater growth than the cervical and thoracic. The slight irregularities in the curve for the sacrum is due to variation in the number of vertebrae in this part (Appendix II). The ribs and sternum follow the thoracic vertebrae fairly closely, being only slightly later developing. The limb bones as a whole, as might be expected from the changes in gross body proportions, are relatively early developing, their rate of increase falling between that of the head bones and the neck and thorax. The pelvis has the greatest proportional increase, if we except the sacrum with which it is functionally connected.

Within the limb bones, those of the upper part—above the cannon bones—make slightly greater relative growth than those below the cannons; this is the case in both fore- and hindlimbs. The major individual bones of the limbs are compared in Table 8 and in Text-figs. 11 and 12.

Several points may be noted here. It is clear that in addition to an anterior-posterior direction in development, the pig, in common with many other vertebrates, exhibits a well-defined centripetal gradient in the rate and order of development of the bones of the limbs. As one proceeds up the limb, the rate of increase of the individual bones over their birth weight increases. Thus the cannon bones make a relatively smaller amount of growth after birth than does the radius-ulna, and the latter a proportionally smaller amount than the scapula. Similarly with the cannons, tibia-fibula, and femur of the hindlimb. The bones of the lower part of the limbs are, therefore, relatively better developed at birth than those of the upper part and, on our definition, must be rated as earlier developing.

The position is very similar to that shown to exist in the sheep (Hammond, 1932a), with one important difference. Compared with the sheep, the limb bones—and indeed all the bones—of the pig are not as well developed at birth. Thus the relative increase in the bones above and

Table 8. *Age changes in bones of limbs*

| | Forelimb | | | | | | Hindlimb | | | | | | | |
Age weeks	Cannons	Splints	Carpals	Radius, ulna	Humerus	Scapula	Cannons	Splints	Tarsals	Cal-caneum	Astragalus	Tibia, fibula	Patella	Femur
							Mean weights (g.)							
Birth	4·2	1·05	2·6	11·0	15·9	7·9	4·2	0·75	1·95	2·6	2·7	11·9	0·8	14·5
4	14·4	3·5	9·5	38·8	51·1	27·9	15·3	3·0	6·7	10·5	11·3	45·8	3·1	57·5
8	26	6·0	19	84	113	65	30	6·0	14·0	20·0	21	89	7·0	124
16	63	16	53	192	285	165	70	13·5	36·5	50	51	227	21	317
20	76	21	59	245	366	224	87	18·0	44·5	62	56	286	23·5	401
24	88	26	76	305	449	281	99	23·7	53·0	74	68·7	360	30	484
28	104	34	82	339	545	350	104	24·0	60·0	79	68	410	35	571
				Relative growth as percentage weight of bone at birth										
Birth	100	100	100	100	100	100	100	100	100	100	100	100	100	100
4	343	333	365	353	321	353	364	400	344	404	419	385	388	397
8	619	571	730	764	711	823	714	800	718	769	778	748	875	858
16	1500	1522	2038	1746	1792	2089	1667	1800	1871	1923	1889	1907	2625	2193
20	1810	2000	2269	2227	2301	2835	2071	2400	2282	2385	2074	2403	2938	2775
24	2095	2476	2923	2773	2824	3557	2357	3160	2718	2846	2544	3025	3700	3349
28	2476	3238	3153	3082	3428	4430	2476	3200	3077	3038	2518	3445	4375	3952
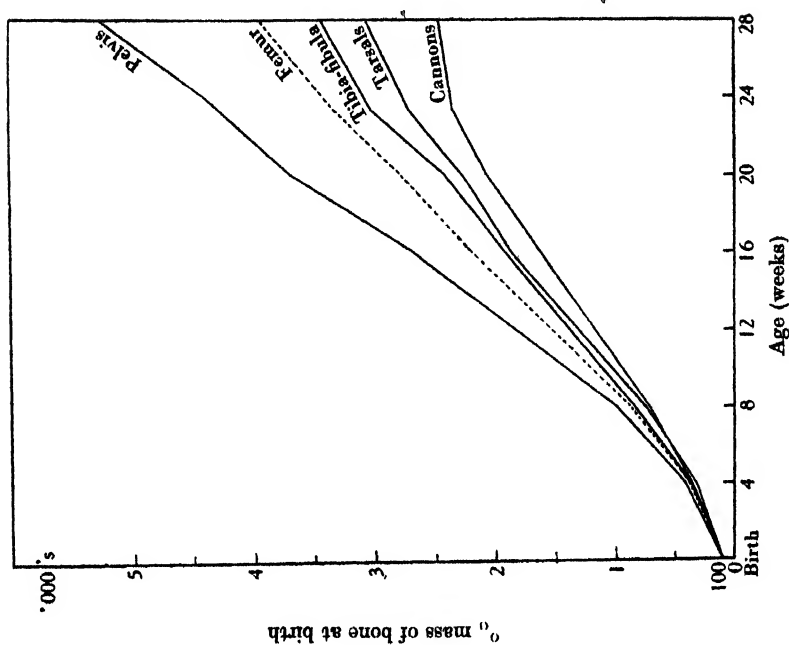
Text-fig. 12. Growth of bones of hindlimbs with age.
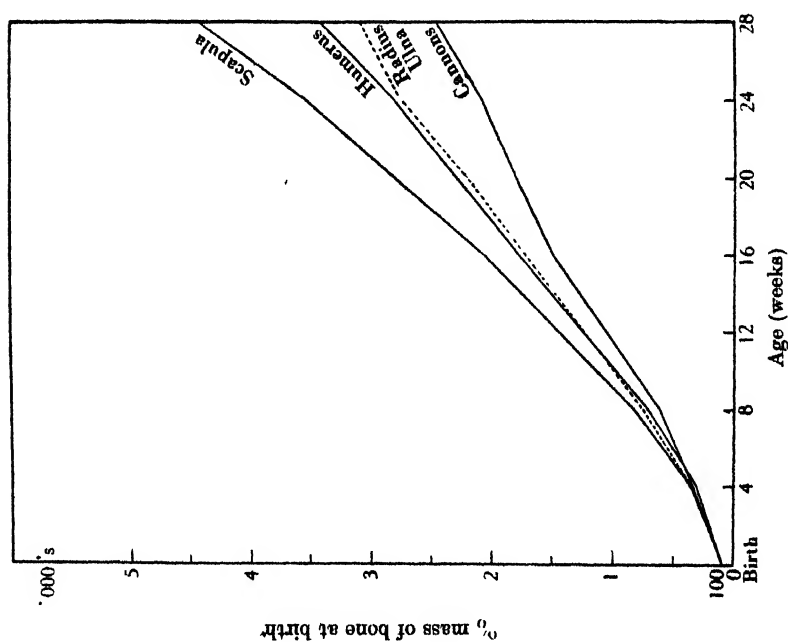
Text-fig. 11. Growth of bones of forelimbs with age.

below the cannons in the hindlimbs are 34·3 and 29·3 times their respective birth weights. Comparable figures for Hammond's sheep but over a much wider age range (birth to 4 years) are 15·1 and 10·4 times. In the pig, then, bone growth is relatively more active in post-natal life. This, apart from the difference in chronological age, would account for the greater steepness of the gradient up the limb bones of the sheep than we find in the pig. Both factors, however, will be operative. This difference in "physiological age" of the bones of the two species would also suggest that since their productive life for meat purposes covers a similar period in time, it should be possible to induce greater post-natal environmental effects upon the skeleton of the pig than of the sheep, whose bones are relatively more advanced at birth.

Changes in form of some of the bones have also been compared photographically (Pl. 1, fig. 2; Pls. 2, 3). In general, growth of bone takes place in two ways: (a) by ossification of cartilages, which is the way in which the majority of bones increase in length, growth occurring mostly between the shaft and the epiphysis; (b) in thickness by additions to, and remodelling of, the bony structure. Thus in the shaft of a long bone, while bone is being absorbed to make room for the development of the bony marrow, it is also being added to on its outer surface.

The shape of the bone is not only related to its weight but is in itself important, since conformation will in part be determined by it. Further, from the meat production point of view, one of the most important considerations is the relationship between length and thickness of the bones. Improvement in the meat-producing breeds has consisted largely in increasing the thickness growth of bones relative to length, the reduction in the ratio being correlated with a greater thickness in the associated muscles (Hammond, 1932a). The probability of these two forms of growth being independent is also suggested by the work of Hammond & Appleton (1932).

In these and all following photographs of bones the background has been ruled in 4 cm. squares. Differences in the size of these between the different plates is due to reduction for practical reasons to different scales. This should be kept in mind in making comparisons. The growth of the skull is shown in Pl. 1, fig. 2. The inclusion of a female at 12 weeks has been made in the series to avoid breaking the continuity; though differences between the sexes exist, these are less in respect of bone than with other tissues, and in any case are not marked at such an early age. At birth the skull of the pig is relatively short and mostly cranium. The facial parts are but poorly developed. The outstanding change in

form is associated with the relatively greater development of the latter. This results in a proportionately greater growth in length than width. The increase in length is most rapid up to about 20 weeks, when it falls off markedly. Since the increase in weight continues at a rapid rate after this age, growth in bone thickness during the later stages, at least, must be proportionately greater than growth in length. The growth of the brain (Table 6) is of interest in relation to these changes; on the one hand its relatively small increase of only 3·0 times its birth weight emphasizes the proportion that the cranium plays to the whole skull at birth, while on the other this increase, relative to the increase of 14·8 times the birth weight in the skull, is indicative of the marked growth in the thickness of the individual bones of the cranial region with age. The latter account for by far the greatest proportion of the total weight of the skull, the facial parts, though long, being thin and light.

The growth of the lumbar vertebrae is shown in Pl. 2, fig. 1. These are specially dealt with since, together with the skull and pelvis (Pl. 2, fig. 2), they form a convenient anatomical group along the trunk line, and because, like the pelvis, they are situated in the most valuable part of the meat animal. As with the skull, length growth is initially rapid but is slowing up at 20 weeks. For the same reasons as indicated in respect to the skull, thickness growth in the lumbar vertebrae must continue at a rapid rate after this time. Growth in width has been greater than in length, the ratio of length to width decreasing over the period. The downward tilt in the transverse processes so pronounced at birth and at the young ages disappears at the older stages, the processes becoming longer and thicker. If, as has been suggested, there is a relation between the thickness of bone and muscle development, increase in the amount of muscle in the loin after about 20 weeks will consist almost entirely of increases in the width and depth of the longissimus dorsi (measures A and B, Text-fig. 2; see also § 8).

In the pelvis (Pl. 2, fig. 2), proportionate increase in length is greater than in the skull, and its rate appears to be also greater during the later stages. As with the lumbar region, however, relative increase in width, as defined by the distance between the acetabula joints, is greater than growth in length. Thickness growth similarly must account for most of the proportionate increase in weight.

No detailed linear measurements of the bones of this series have been made so that no precise description of changes in form is attempted. In view of our special interest in length and thickness growth however, the maximum length of the cannon bones and the femurs of the pigs at

each age has been recorded. The weight/length ratio of the bone has then been taken as an index of thickness growth. The results are shown in Table 9 and the bones themselves in Pl. 3.

Table 9. *Relative length and thickness growth in bone with age*

	Birth	4 weeks	8 weeks	12 weeks	16 weeks	20 weeks	24 weeks	28 weeks
Cannon bone:								
Length	100	143	202	245	278	320	327	336
Weight/length	100	255	354	400	599	646	720	736
Femur:								
Length	100	154	217	253	287	329	345	370
Weight/length	100	257	394	477	761	840	968	1065

The relative growth in length is proportionately smaller than in thickness in both cases. The figures support the findings of Hammond & Appleton (1932) as to the late developing character of thickness growth. Note also that the relative growth in both length and thickness is proportionately greater in the later developing femur. This situation is also clearly illustrated in Pl. 3, where practically no increase after 20 weeks occurs in the length of the cannon bones, while the femur continues to lengthen though at a decreasing rate. If one considers the pelvis as equivalent to the scapula and as part of the hindlimb bones, the centripetal order in development is seen to follow right through to the vertebral column.

(6) Relative development of muscles in different parts of the body

As with the bones, the muscles of any one area grow at a different rate from those of another area. The method of dissection employed allows some comparison between the major anatomical muscle groups, and the relation of their manner of growth to that of the body as a whole and to the trends exhibited by other parts and tissues. Table 10 sets out the mean weight and the relative growth of the muscles as a percentage of the weight of the part at 4 weeks.

The 4-week base-line has been taken in this case, because of the technical difficulty of securing precision in the jointing of the birth pig and the small number of the latter available in this series. Text-fig. 13 shows the resulting curves for the muscles of the head and trunk, and Text-figs. 14 and 15 those for the fore- and hindlimbs.

The musculature of the head and trunk show a similar trend to that noted in respect to the related bone groups—a greater rate and amount

Table 10. *Age changes in muscles of different parts of body*

Age weeks	Head	Neck	Forelimb			Thorax	Loin		Hindlimb			Pelvis
			Shoulder	Arm	Cannon		Psoas	Loin	Thigh	Leg	Cannon	
						Mean weights (g.)						
4	81	172	376	54	2·6	459	35·5	133	385	85	4·0	115·6
8	176	321	922	117	6·0	852	58	282	920	180	9·0	219
16	577	977	2399	253	11·5	2898	284	1217	2631	474	19·0	931
20	659	1557	3144	352	16·5	4112	385	1470	3825	728	28·0	1444
24	880	1971	4234	448	20·0	5348	520	1935	4877	934	30·0	1817
28	1016	2476	5528	590	23·0	7875	652	3221	6738	1151	46·0	2331
						Relative growth as percentage weight of part at 4 weeks						
4	100	100	100	100	100	100	100	100	100	100	100	100
8	217	187	245	217	231	186	163	212	239	213	225	189
16	712	568	638	469	442	631	800	915	683	560	475	805
20	814	905	836	652	635	896	1084	1105	994	862	700	1249
24	1086	1146	1126	830	769	1165	1465	1457	1267	1105	750	1572
28	1254	1440	1470	1092	885	1716	1837	2422	1750	1362	1150	2016

of growth with age as one proceeds from the fore to the hind end of the body. The differences are not as sharply defined nor the curves as regular as in the bones; this is due, probably, partly to the small numbers of animals used and to the greater variability necessarily associated with a later developing tissue than with an earlier developing one. In general the results, however, substantiate our general picture of an anterior-posterior order in development. The head muscles grow proportionately
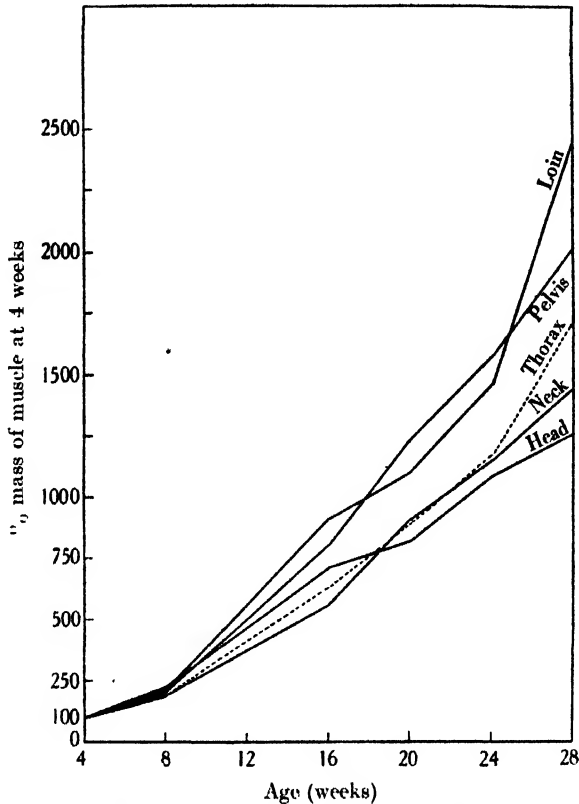
Text-fig. 13. Growth of muscles of trunk with age.

least, and those of the loin and pelvis region proportionately most, with the neck and thoracic muscles falling into an intermediate position.

Similarly in the case of the limb muscles. Those lying round the scapula and humerus (shoulder muscles) show a greater relative increase than those surrounding the radius-ulna (arm muscles). The latter grow at a faster rate than those around the metacarpal bones (cannon). In the hindlimb a similar order in development from the lower to the upper group of muscles is observed. Those lying round the femur develop

%o mass of part at 4 weeks
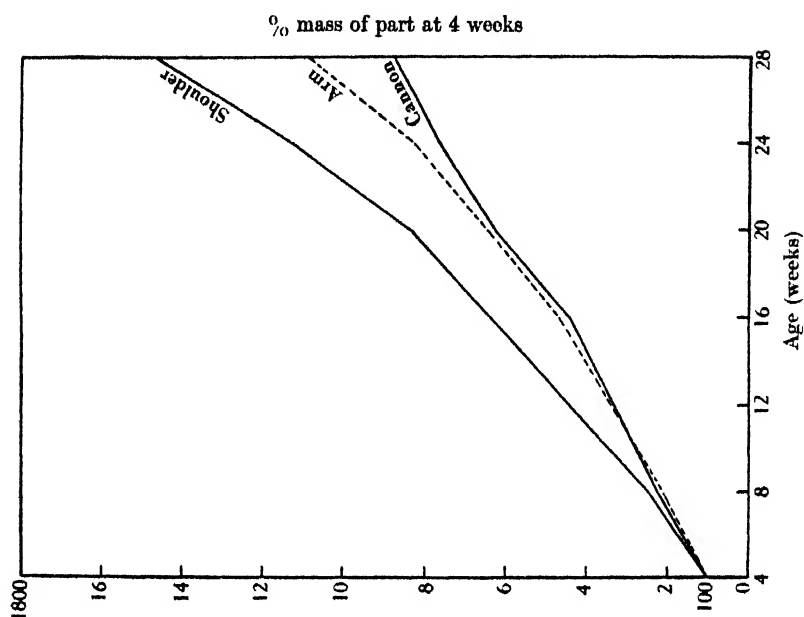
Text-fig. 15. Growth of muscles of forelimbs with age.

% mass of part at 4 weeks
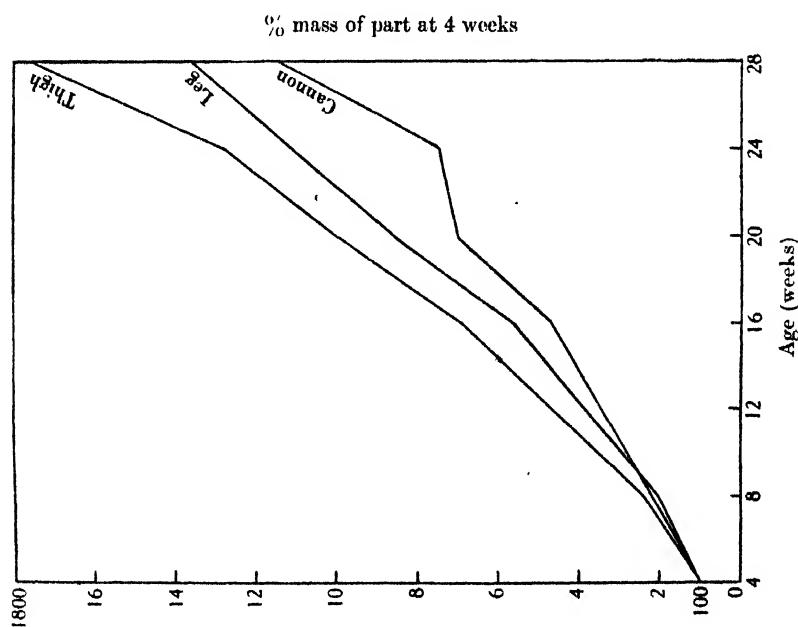
Text-fig. 14. Growth of muscle of hindlimbs with age.

more after 4 weeks than those around the tibia-fibula, and the latter more than those about the hind cannons. The differences are comparable to the similar rate of growth of the bones of these areas.

Hammond & Appleton (1932) have drawn attention to similar differences in the sheep, and in addition have shown that within these groups (in the hindlimb) marked differences in the rate of growth of individual muscles occurs. The length growth of a muscle naturally follows that of the bone round which it lies, and as in bones, thickness growth of muscle develops later than length growth (see Carcass measurements *A* and *B*), and seems also to be linked with thickness growth in the bone.

(7) Relative development of fat in different parts of the body

The age changes in the growth of the fat have been similarly compared in Table 11 and Text-fig. 16. A 4-week base-line has again been used for the reason already given. Fat is subdivided into subcutaneous— which comprises the greatest bulk at all ages, and the intermuscular. The total carcass fat is also shown. The latter of course excludes intramuscular fat which can only be determined chemically.

The growth of fat must be regarded from a different point of view from the growth in other tissues. Its production is, for the main part, not vital to the existence of the animal, except probably in very early life when, as already suggested, its temperature-regulating function is perhaps important. Its main purpose is that of nutrient storage, and the extent of its development is largely indicative of the nutritional level of the organism. Its production, however, is a normal part of the phenomenon of growth in meat animals, and the extent and distribution of its growth throughout the body is an extremely important aspect of meat quality.

The late developing character of fat as a whole has already been commented on, and the data here presented show that like the other tissues, its growth in different parts of the body also varies.

By far the greater proportional increase occurs in the hind parts of the trunk; the order of development is the same as that for muscle and bone. Fat of legs and shoulders similarly develops at a rate intermediate between that of the neck and thorax in the case of the forelimb and at a comparable though slightly faster rate in the hindlimb.

Some evidence is available also of a directional order up the leg, in

that the intermuscular fat of the lower part of both limbs increases proportionately less with age than that of the upper parts. Subcutaneous fat is available only for the limbs as a whole.

Note that although the actual increase in the amount of subcutaneous fat far outstrips that of the intermuscular, the relative increase is greater in the latter. This applies to each individual joint as well as to the whole. In general terms it seems that fat is not stored between the muscle to any extent until the later stages of growth, while it may be deposited subcutaneously in large amounts well before this stage. This does not, however, appear to be the whole story. Differentiation into

Table 11a. *Age changes in fat in different parts of the body*

	Mean weights (g.)					
	4 weeks	8 weeks	16 weeks	20 weeks	24 weeks	28 weeks
Head:						
Subcutaneous	89·5	135	520	720	701	1400
Intermuscular	39·3	77	250	311	377	922
Total	128·8	212	770	1031	1078	2322
Neck:						
Subcutaneous	86·5	137	392	1049	1559	1451
Intermuscular	27	65	314	468	722	1345
Total	113·5	202	706	1517	2281	2796
Forelimbs:						
Subcutaneous	139	346	835	1186	2063	3159
Intermuscular (sh.)	27·5	22	297	442	678	1075
Intermuscular (arm)	4·0	5	15	67	66	87
Total	170·5	373	1147	1695	2807	4321
Thorax:						
Subcutaneous	213	496	1434	2830	4757	7216
Intermuscular	50	85	671	1368	2292	4838
Total	263	581	2105	4198	7049	12054
Loin:						
Subcutaneous	113	191	888	1475		4740
Intermuscular	12·6	18	166	164		1109
Total	125·5	209	1054	1639	2623	5849
Pelvis:						
Subcutaneous	44	61	411	1140	2022	2473
Intermuscular	10·2	17	81	234	255	605
Total	54·2	78	492	1374	2277	3078
Hindlimbs:						
Subcutaneous	108	294	689	1425	2312	3406
Intermuscular (thigh)	16	20	133	250	336	588
Intermuscular (leg)	6·4	5	35	59	91	99
Total	130·4	319	857	1734	2739	4093
Total:						
Subcutaneous	792	1660	5167	9824	15690	23845
Intermuscular	192	314	1960	3362	5164	10668
Total	984	1974	7127	13186	20854	34513

Table 11 b. *Age changes in fat in different parts of the body*

Relative growth as percentage weight of fat at 4 weeks

	4 weeks	8 weeks	16 weeks	20 weeks	24 weeks	28 weeks
Head:						
Subcutaneous	100	150	581	804	783	1564
Intermuscular	100	196	636	791	959	2346
Total	100	164	597	799	837	1800
Neck:						
Subcutaneous	100	158	453	1212	1802	1678
Intermuscular	100	241	1162	1733	2674	4981
Total	100	177	619	1330	2000	2453
Forelimbs:						
Subcutaneous	100	249	601	853	1484	2273
Intermuscular (sh.)	100	80	1084	1607	2465	3909
Intermuscular (arm)	100	125	383	1675	1650	2175
Total	100	219	673	994	1646	2534
Thorax:						
Subcutaneous	100	232	673	1328	2233	3387
Intermuscular	100	170	1342	2736	4584	9676
Total	100	220	800	1596	2680	4583
Loin:						
Subcutaneous	100	169	786	1305	2014	4194
Intermuscular	100	142	1317	1300	2753	8801
Total	100	165	837	1300	2081	4662
Pelvis:						
Subcutaneous	100	139	934	2590	4595	5620
Intermuscular	100	167	794	2294	2500	5931
Total	100	181	1142	3195	5295	5679
Hindlimbs:						
Subcutaneous	100	272	638	1319	2141	3153
Intermuscular (thigh)	100	125	831	1593	2100	3675
Intermuscular (leg)	100	78	547	922	1421	1546
Total	100	245	658	1333	2107	3148
Total:						
Subcutaneous	100	209	652	1240	1981	3010
Intermuscular	100	163	1021	1751	2707	5556
Total	100	200	724	1340	2123	3507

intermuscular and subcutaneous fat is a somewhat arbitrary classification, based on anatomical position rather than on function, which is probably the more logical basis. Included in the former, in all joints, there is in consequence a large proportion of fat with the "permanent" storage character of subcutaneous as distinct from the fat lying between muscles engaged in movement. The latter is clearly different in its physical characters; it covers moving muscle surfaces and fills the spaces between bone and muscle points of attachment. It thus appears to have more the function of buffering or reducing friction and of providing an immediate reserve of energy rather than to be a more permanent reserve. This type

is perhaps more precisely to be described as intermuscular; it is present in relatively large amounts even in the young animals, and increases relatively less with age than "true" storage fat. Particularly in such joints at the neck, thorax, and loin, however, there is deposited between the relatively little used surface muscles large quantities of the latter type of fat, particularly during the later stages of growth. The inclusion
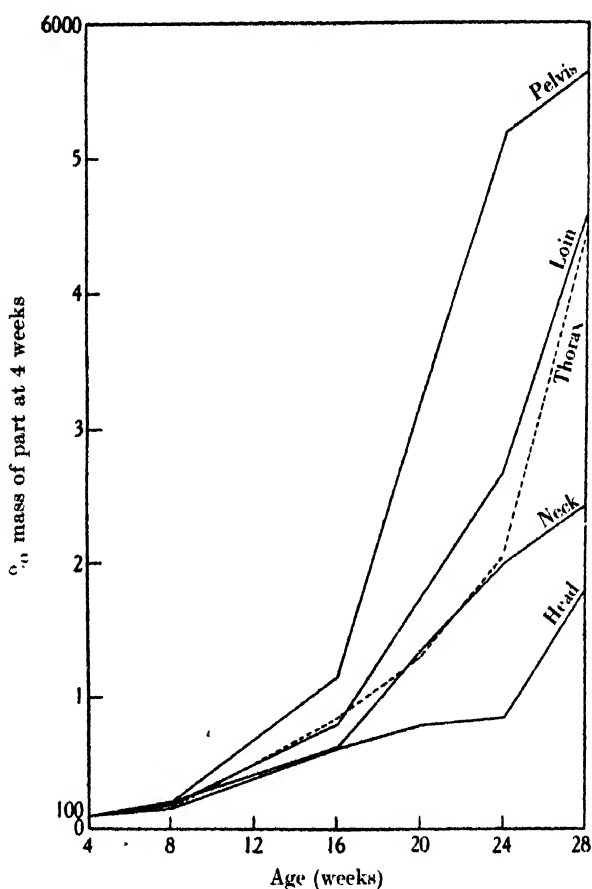
Text-fig. 16. Growth of fat of trunk with age.

of this as intermuscular is responsible for the greater relative development of this tissue, as compared with subcutaneous. Only in the intermuscular fat of the lower arm of the forelimb, and the leg of the hindlimb, is such fat not present. Here we find the relative increase with age less than that of subcutaneous. This situation is important in view of certain differences in the behaviour of these two types of fat under experimental treatments later described.

In fat, as in other tissues then, we find differential rates of growth in different parts of the body and that these exhibit an orderly behaviour in line with those of muscle and bone.

(8) Changes in body and carcass measurements

The relationship of changes in body and carcass measurements to the changes we have noted in carcass composition with age are of special interest. It has long been the practice to evaluate the commercial quality of pig carcasses on the basis of certain measurements. Thus most countries interested in pig production have "grading standards" designed for the special quality requirements of the trade in which they are concerned. Further, the performance ability of breeding stock is frequently assessed on a similar basis. The actual measurements used for the purpose are in the main confined to some measure of the length of the carcass and to the proportion of fat in it, and the particular measures employed are believed to bear a general relationship to the composition of the body. The precise situation in this respect has been the subject of a special investigation and is dealt with in a later section of this paper. At this stage it will suffice to note that measures of back-fat thickness play a dominant part in all such standards, and that these have been shown by Hankin & Ellis (1934) to be related to the chemically determined amount of fat in the body. Little attention has been paid to indices of muscle, though an advance in this direction has been made recently by Davidson et al. (1936) who have proposed methods now used by several countries for this purpose.

For the moment it will be our main concern to compare the changes with age in those measures commonly used and in others that we have taken, and to show these are intelligibly related to changes in form and composition.

The mean measurements concerned, and their relative increase with age are shown in Table 12 and in Text-figs. 17 and 18. Of the "external" measures, those on the legs increase relatively less than those on the trunk, and those of the lower part of the limbs less than those of the upper part or of the limb as a whole. Thus the length of the foretrotter appears to be the earliest developing measurement taken, followed by the length of the forearm, and the length of the hindleg, in that order. Thickening growth in the leg, as measured by the circumference of the forearm, increases relatively more than any of these. Such changes are in line with those we have already noted in the mass of the limbs as a

Table 12. *Age changes in body and carcass measurements*

| Age weeks | Body length | Carcass length | Chest depth | Leg length | Length trotter | Forearm | | Thickness back fat | | | Mean belly thickness | Cut at last rib | | | | Thickness skin |
						Length arm	Circum. arm	Shoulder	Loin	Rump		Length eye, A	Depth eye, B	Fat at C	Fat at H	
								Mean measurements (mm.)								
Birth	264	189	80	168	36	60	61	5·0	2·0	2·0	3·75	24	6·5	2	2	1
4	403	305	127	255	52	94	106	16·5	6·5	7·6	10·8	36·5	11·5	6	9	2
8	—	415	175	345	70	—	—	26·0	7·0	10·0	12·0	57	15	8	12	2
16	845	621	247	475	91	157	167	25·5	9·5	13·7	20·3	66	29	10	16	2
20	972	689	289	525	102	188	193	38·0	16·5	23·0	23·5	75	31	18	23	2
24	1017	719	327	547	91	202	218	38·0	19·0	30·0	24·5	80	34	22	34	2·3
28	1110	797	397	590	106	202	222	48·0	37·4	42·0	36·3	75	49	39	44	3·0
						Proportional development as percentage of measurement at birth										
Birth	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100
4	153	161	159	152	144	157	174	330	325	380	288	152	177	300	450	200
8	—	220	219	206	194	—	—	520	350	500	320	238	231	400	600	200
16	320	329	309	283	253	262	274	510	475	685	488	275	446	500	800	200
20	368	365	361	313	283	313	316	760	825	1150	627	313	477	900	1150	200
24	385	380	409	326	253	337	357	840	950	1500	653	333	523	1100	1700	230
28	420	422	496	351	294	337	364	960	1850	2100	968	313	754	1950	2200	300

Text-fig. 18. Age changes in carcass measurements, loin cut and streak.

Text-fig. 17. Age changes in carcass measurements.

whole and in the tissues forming them. Length growth will be related with the development of bone and thickness growth to increase in muscle and fat which occurs at a relatively greater rate during the later ages.

The total length of the body and the length of the carcass follow a similar curve, and the relative small increase of 4·2 times the birth measurements in each case emphasizes the early developing nature of length growth. The rate of increase (Text-fig. 17) in length falls rapidly after the 16-week stage. The depth of the chest continues to increase at a rapid rate during this period.

Of the internal measurements, changes in back-fat thickness are relatively large and in line with what we have found to occur in respect to the mass of this tissue. The relatively greater increase in the loin and rump-fat measures too, as compared with the shoulder fat, are comparable to the similar changes in the mass of fat as one proceeds from the head to tail. The subcutaneous back fat of the pig is clearly differentiated into two layers by a line of connective tissue. Since these two layers are qualitatively different (Callow, 1935), their relative growth is of interest. The ratio of inner to outer fat increases markedly with age (Table 13).

Table 13. *Changes in ratio of shoulder and loin fat measurements with age*

		Birth	4 weeks	8 weeks	16 weeks	20 weeks	24 weeks	28 weeks
Shoulder:	Inner/outer	100	230	160	240	250	322	336
Loin:	Inner/outer	100	63	75	90	120	171	236
Inner fat:	Shoulder/loin	250	460	533	401	277	242	142
Outer fat:	Shoulder/loin	250,	125	250	150	133	128	100
Total:	Shoulder/loin	250	254	371	268	230	200	130

The outer layer is laid down relatively early in life and increases little. It also tends to be more uniformly distributed over the body than the inner layer in which by far the greater proportion of the increase in fat is deposited. The ratio of shoulder to loin fat is of interest in relation to the relative weight given to one or other of these measures in assessing quality. Note (Table 13) that the rate of fat deposition is initially greater at the shoulder, the ratio increasing up to 8 weeks. After this stage the maximal rate passes along the back line and the thickness of loin fat increases proportionately more and the ratio falls. This occurs both in respect to inner and outer layers. As suggested by Callow (1936), the magnitude of the shoulder fat/loin fat ratio might thus be used as an index of the stage to which fattening has progressed

and for the same reason, the loin fat measure may provide a more effective index of fatness (see also Davidson *et al.* 1936, and Hammond & Murray, 1937).

The thickness of the "streak" or "belly"—an important measure in relation to the quality of bacon pigs in that it provides an index of the size of the bacon rasher from this region—shows up in comparison with the other measurements as a relatively late developing character. This situation is largely due to the fact that much of the increased thickness here is composed of fat.

Measures on the loin cut at the last rib (Text-fig. 1) provide some index in respect to muscle changes as well as fat (Table 12). The "length of the eye"—measure *A*—is relatively earlier developing than the "depth"—measure *B*, the latter increasing at a greater rate from 8 weeks onwards, with an increasing difference during the later ages. This is in line with the suggestion already made that thickening growth in the muscle is a relatively late developing character. Hammond (1936*b*) has shown a similar situation to exist in the shape of the longissimus dorsi in sheep and cattle as well as in pigs with increased body weight. The relative increases in these measures, however, are less than those in fat on the same cut. Fat at *C* and fat at *H* both give increases characteristic of fat and to an extent comparable with the loin and rump back-fat measures respectively. Note the greater rate of growth of *H*—a measurement which in view of its position has a special qualitative significance (see Davidson *et al.* 1936 and Part IV).

The thickness of skin increases relatively little over the age period studied, a result in line with our data for its increase in weight.

(9) Histological changes in muscle with age

The histological changes in the muscles of the pig are of direct interest not only in relation to the growth in weight of the tissue, but also in respect to quality of the carcass. Hammond & Appleton (1932) have given an extensive survey of the literature on the subject, and in addition have provided much data in respect to sheep. In the development of muscle, as in other tissues, growth occurs first by increase in the number of cells, and later by increase in cell size. It seems generally agreed that in the wide series of animals studied by different workers, growth of muscle occurs mostly by hyperplasia in pre-natal life and by hypertrophy in post-natal, though the time at which formation of new muscle cells ceases is not known definitely for the different species.

Table 14. *Age changes in muscle fibre diameter*

Muscle ...	Rectus femoris			Gastrocnemius			Longissimus dorsi		
Age weeks	Mean diameter μ	Level of sig-nificance	c.v. %	Mean diameter μ	Level of sig-nificance	c.v. %	Mean diameter μ	Level of sig-nificance	c.v. %
Birth	2·54±0·154	<0·01	42·5	2·32±0·181	<0·01	54·7	2·58±0·161	<0·01	43·6
4	4·12±0·131	<0·01	22·3	4·20±0·216	<0·01	36·0	4·88±0·209	<0·01	30·0
8	6·24±0·317	<0·01	35·8	7·50±0·362	<0·01	33·7	6·56±0·287	<0·01	30·6
16	10·08±0·699	<0·01	48·6	9·82±0·221	<0·01	15·7	10·74±0·373	<0·01	24·3
20	14·3 ±0·516	N.S.	23·1	15·62±0·538	<0·01	24·1	16·22±0·491	<0·05	21·2
24	14·46±0·464	<0·01	22·4	17·98±0·534	<0·01	21·0	17·06±0·486	<0·01	20·0
28	20·5 ±0·588		20·1	22·04±0·809		22·9	21·50±0·768		25·0

N.S. = Not significant.

We have measured the size of the muscle fibres at the different ages of the series of pigs under consideration, and have also endeavoured to ascertain whether increase in numbers of fibres occurs after birth by counting the numbers of these per bundle. Three separate muscles have been dealt with; the gastrocnemius surrounding the tibia, the rectus femoris, round the femur, and the longissimus dorsi sampled at the junction of the loin and thorax. In the first two, the samples were also taken from the centre of the muscle. While differences in the size of the fibre occurs along its length, sampling at the same position gives comparative results. Measurements were made by cutting freehand shavings of the muscle with a razor, after fixation in 10 % formalin. The shavings were stained with picric acid, and mounted in Farrant's solution. This technique resulted in the separation of short lengths of individual fibres so that each retained its natural shape. Measurements were recorded of the cross diameter of fifty fibres in each muscle with an eyepiece micrometer; two slides were prepared from different parts of the sample and twenty-five fibres taken from each

The results are shown in Table 14 in the form of mean diameter at each age, standard errors, and coefficients of variation. The significance of the increase with age has been tested by means of the "*t*" test (Fisher, 1934).

In each muscle, fibre diameter size significantly increases with age. The extent of the increase—over eight times in diameter and seventy times in cross-section area—is sufficient to account for most of the increase in weight of muscle tissue over the same period.

A considerable variation in fibre size is apparent at each age; the coefficient of variation, however, decreases fairly consistently with age. This is in line with the theory that post-natal growth is one of hyper-

trophy, an increasing proportion of the fibres approaching the limits of their size as growth proceeds. No consistent significant differences were found between fibre size in the three muscles studied. From the results of other workers one might reasonably expect to find a larger fibre size in those muscles (longissimus dorsi) making greater proportional growth after birth, than those making smaller growth (gastrocnemius). Our failure to do this may be due to the relatively short age period covered (see development of skeleton) and/or to the relative difference in the length growth of the different muscles. It will be obvious that differences in the length of the muscle fibre are associated with differences in diameter in affecting increase in weight.

For counting the number of fibres per muscle bundle, cross-sections were prepared by cutting with the paraffin method. Sections were stained with picric acid and others from the same muscle with ˌVan Geison's stain. The latter was employed to show up the connective tissue and to locate, if present, the pigment granules reported from the muscles of other animals by many workers (see Hammond & Appleton, 1932). The fibres of twenty bundles, selected at random, were counted from each muscle. The results are shown in Table 15.

Table 15. *Age changes in number of muscle fibres per bundle.*
(*Mean number of fibres in sample of twenty bundles*)

Age (weeks)	Rectus femoris	Gastrocnemius	Longissimus dorsi
Birth	47·8 ± 20·3	47·7 ± 22·8	44·5 ± 18·3
4	32·9 ± 16·2	46·9 ± 19·5	40·7 ± 17·8
8	49·7 ± 28·0	50·5 ± 25·2	50·9 ± 22·7
16	47·5 ± 24·4	56·4 ± 19·4	49·1 ± 21·7
20	50·1 ± 25·2	47·6 ± 22·2	51·2 ± 29·0
24	69·9 ± 26·0	48·8 ± 28 7	52·0 ± 26·9

These fully bear out the suggestion as to muscle growth after birth occurring mostly, if not entirely, in fibre size. It is not possible to differentiate between the number of fibres per bundle either with age or between the three muscles studied.

The variation in the number is extremely high, the standard deviations actually exceeding the mean figure in each case.

From the meat quality viewpoint, the importance of the size of the muscle fibre lies in its relation to tenderness of the meat. Muscles with small fibres are more tender than those with large, hence the increasing toughness with age. Tenderness is also associated with the size of the muscle bundle—the grain of the meat. Variations in the size of the latter are due, as seen by our figures, to both number and size of fibres,

though the increase in the size of the bundle with age would appear to be a matter of fibre size increase only.

The sections stained with Van Geison were carefully examined for presence of pigment granules previously referred to. None were found. This would appear to support the hypothesis of Hammond & Appleton (1932) that such granules are breakdown products of haemoglobin resulting from the fixation with formalin. The muscles of the pig are extremely pale in colour, indicating a low level of muscle haemoglobin, and this is specially the case in young animals as in this series.

Colour of muscle is related to flavour, the darker the meat the stronger the flavour. It is not an important quality character in the pig, such as it is in veal and beef, though generally a pale colour is preferred specially in the fresh pork trade. Colour is due to the presence of muscle haemoglobin which has a fatigue-resisting function (Millikan, 1936) and which in consequence both increases with age and with exercise (Needham, 1926). To test the latter points, the colours of a muscle subject to constant exercise (diaphragm), and of the normally used relatively less and typical of the edible flesh (longissimus dorsi) have been compared (Table 16). These were judged by eye by two independent

Table 16. *Changes in colour of muscle with age*

	Birth	4 weeks	8 weeks	16 weeks	20 weeks	24 weeks	28 weeks
Longissimus dorsi (at last rib)	2 (P)	2 (P)	4 (P)	3·5 (P)	4 (P)	3 (P)	3 (P)
Diaphragm	2 (P)	2 (P)	5 (P)	5 (P)	9 (B)	9 (B)	9 (B)

1 = Pale; 12 = Dark.

$$P = \frac{\text{Pork scale}}{1-5}; \qquad B = \frac{\text{Beef scale}}{6-12}$$

observers, using a specially prepared colour scale. It will be noted that the diaphragm is much darker in colour after 4 weeks, so much so that at 16 weeks it runs off the "pork scale" and reaches a high figure on the "beef scale". The value "nine" on this corresponds to a dark red, while "two" on the pork scale is almost colourless and the maximum value "five" only a few tones darker. On the other hand, the longissimus dorsi shows low figures throughout on the pork scale, with but a slight increase with age.

Cross-sections of the longissimus dorsi were also prepared by the freezing method and stained with Sudan III to show up intramuscular "marbling" fat. Marbling in beef is an important quality character; it is less important in sheep but so far as is known is of no commercial

significance in pork or bacon. Its behaviour is none the less interesting especially in relation to the fat-quality problem (see § 10), and the general growth of fatty tissues. A photographic series showing the increase in the amount of marbling fat with age is shown in Plate 4. These are direct prints from the slides and so the fat shows up as white streaks. Note that no definite areas of fat are apparent in the new-born and the 4-week animal, while a small amount only is present in the 8-week. Though this is so, high-power examination of the muscle tissue of the birth, 4-week, and 8-week pigs revealed the presence of large numbers of apparently free-fat globules distributed throughout certain of the muscle fibres. These have been stained and their presence may be observed in the photographs (Pl. 5). These globules gradually decrease in number with age until at 16 weeks and subsequent ages they could no longer be detected. The presence of this fat at the birth and 4-week stage is confirmed by its chemical extraction at these ages. It would appear that the muscular tissues of the new-born pig are provided with an immediate supply of fat presumably for metabolic purposes, and that as growth proceeds these supplies disappear. So far as we are aware, this phenomenon has not hitherto been reported.

(10) AGE CHANGES IN CHEMICAL COMPOSITION

While our main purpose is to indicate the changes which occur in the form and weight of the tissues comprising the body of the pig, changes in chemical composition have not been neglected. These, though less directly—or it might be more reasonably argued—less obviously associated with meat quality, are nevertheless of considerable importance. The nutritive value of meat is dependent partly upon its composition in terms of water, fat, protein, and mineral matter. The chemical nature of the fat too, is of some consequence, particularly in respect to the bacon pig. Its degree of saturation is associated with important qualitative effects such that the problem of "soft" fat is a serious one in relation to appearance, cooking losses, freezing, storage and transport, and curing. Unsaturated fat is more reactive, chemically, than saturated fat, and therefore liable to develop rancidity. Rancidity changes are catalysed by light, and by the salts used in curing (Lea, 1931, 1934), so that bacon fat is specially susceptible. Unsaturated fat for the same reasons will not stand up to long periods of storage and transport as is frequently necessary. These, and other aspects are discussed by Callow (1935 a, b), who has recently reviewed the extensive literature on the subject.

All the chemical aspects of these studies have been in the hands of

Dr E. H. Callow of the Low Temperature Research Station, Cambridge, to whom we are indebted for the data reported. At the present stage these are necessarily limited; the volume of work resulting from our age series and associated experiments will require several years to complete, so that until final results are to hand, even the few observations made must be regarded as tentative. Some of the data referred to have already been published and reference to these is made as they occur.

Table 17. *Age changes in chemical composition*

(a) *Fat*

| | Internal fat | | | Back fat (subcutaneous) | | | | | |
| | Kidney and flares | | | Outer layer | | | Inner layer | | |
Age weeks	% fat	% tissue	% water	% fat	% tissue	% water	% fat	% tissue	% water
Birth	—	—	—	6·22*	8·89*	84·89*	6·22*	8·89*	84·89*
4	72·67	6·37	21·01	75·37	5·11	19·52	76·84	4·66	18·50
8	71·20	8·84	19·96	76·69	6·65	16·66	76·90	8·01	15·09
16	85·55	4·52	9·93	84·45	6·41	9·14	87·79	4·84	7·37
20	84·08	3·05	12·87	85·91	3·89	10·20	90·72	2·72	6·56
28	93·86	1·19	4·95	92·44	2·63	4·93	94·33	1·90	3·77

| | Back and belly fat (subcutaneous) | | | | | |
| | Outer layer | | | Inner layer | | |
Age weeks	% fat	% tissue	% water	% fat	% tissue	% water
Birth	—	—	—	—	—	—
4	74·02	4·72	17·26	82·79	3·72	13·49
8	70·73	10·09	19·18	86·74	3·12	10·14
16	74·88	10·46	14·66	87·50	3·36	9·14
20	87·11	3·64	9·25	91·91	2·09	6·00
28	92·82	2·48	4·70	96·43	1·19	2·38

* Inner and outer layer bulked owing to small size of sample.

Changes in the chemical composition of the pig with increasing weight and age have been studied by Ellis & Hankins (1925), Mitchell & Hamilton (1929), Scott (1930) and Schmidt & Zimmerman (1934) in the course of nutritional investigations. Wood (1926) also presents a limited amount of data. In general terms, these show that in the pig, as in other animals, the percentage of dry matter and fat increases, and the percentage of water, protein, and ash decreases with age and weight. Callow (1935a), from Ellis & Hankin's figures, has produced curves indicating the three phases of growth in chemical composition; the first phase when ash is growing more rapidly than at any other period; the second when growth in protein (muscular tissue) predominates; and the last when the rate of deposition of fat reaches a maximum. The agreement between these and

the changes we have found in "anatomical" composition might be noted.

The chemical composition of our age series in terms of percentage fat, tissue and water, is shown for the major fat tissues (Table 17) and for the muscle tissue (Table 18).

The kidney fat and flares have been taken as representative of the "internal fat" reserves, and the back fat (a strip running from head to tail) and back and belly fat (a strip running from the mid-back line at the junction of loin and thorax to the median belly line) as representative of the subcutaneous fat. The inner and outer layers of the latter have been dealt with separately except in the birth animals where this was impracticable. Figures given represent mean values for these deposits.

In all fatty tissues, the percentage fat increases with age; this increase is initially extremely rapid—between birth and 4 weeks—but after the rate is much slower. Considering the small number of individuals involved the behaviour is fairly consistent. The percentage of fat at all ages, and in both back and belly regions, is greater in the inner layer than in the outer layer. Callow (1935b, 1937) has analysed these figures in greater detail and shown that a gradient from head to tail occurs in the percentage of fat in both inner and outer layers of subcutaneous fat. The percentage fat falls as one passes backwards along the body. The change with age is such that the relative difference between the percentage fat in the fore and hind ends decreases, indicating a greater rate of deposition in the hind end as compared with the fore as fattening progresses. This situation fits well with our picture of an anterior-posterior gradient in the rate of growth of the fat.

The percentage tissue (dry weight of fat-free connective tissue) and the percentage of water both decrease with age. The former, however, show an increase between 4 and 8 weeks. This is due to differences in the relative rate of fat deposition and growth of connective tissue (Callow, 1935b). The former grows at the same or at even a faster rate during the period but later the relative rate of fat deposition is much greater, and the percentage tissue falls.

The figures for water show up the marked drop between birth and 4 weeks, and the general fall with age.

Changes in the composition of the muscles (Table 18) follow a similar trend to those in the fat. The percentage of fat (intramuscular) in the psoas muscle and the longissimus dorsi (mean of five samples along the back line) shows a general increase with age. In both muscles a marked drop occurs after the initial birth to 4-week rise. As in the case of fat

Callow (1935*b*) has explained this in terms of differences in the relative growth rates of fat and muscular tissue. During the younger ages, muscle tissue is growing fast relative to fat, but later the rate of fat deposition overtakes it, and the percentage fat increases. The percentage water is much higher in muscle tissue than in fat, while it does not exhibit the extremely large drop between birth and 4 weeks, but rather declines at a fairly steady rate throughout the period. The percentage residue (dry weight of muscle tissue) increases with age.

Table 18. *Age changes in chemical composition*

(*b*) *Muscle*

	Psoas muscle				Longissimus dorsi			
Age weeks	% fat	% residue	% water	% water fat-free basis	% fat	% residue	% water	% water fat-free basis
Birth	2·12	17·14	80·71	82·45	1·92	16·61	81·47	83·05
4	3·77	19·42	76·81	79·82	4·32	19·92	75·75	79·17
8	2·80	19·39	77·81	80·05	4·73	19·05	76·22	80·00
16	2·48	21·20	76·32	78·26	3·39	20·95	75·66	78·31
20	2·18	21·50	76·32	78·02	4·02	21·61	74·37	77·48
28	3·00	23·23	73·77	76·05	5·62	22·61	71·77	76·04

A similar gradient to that in fat along the back line is exhibited in the growth of the intramuscular fat (Table 19). The percentage of fat is always higher at 2 months than at 3, but the amount of the difference between the percentages at the two ages is not the same at all points along the back. The differences are greatest at the head and least near the tail. Changes in the iodine number are shown in Table 20. Not only does the proportion of fat in the tissues alter with age, but its chemical nature undergoes progressive changes. In all cases the fat becomes less saturated up to the 8-week stage; after this it becomes more saturated and the iodine number drops. The decrease in the iodine number with age during the later stages of fattening can also be explained on a basis

Table 19. *Percentage of fat in muscles of the back between 2 and 3 months (from Callow, 1935)*

Position of muscle	2 months	3 months	Difference
Near head	8·5	4·2	4·3
	6·3	2·0	4·3
	4·2	0·7	3·5
	2·6	1·4	1·2
Near tail	2·0	1·3	0·7
Psoas muscle	2·8	2·1	0·7

of the increased rate of fat deposition during this period (Callow, 1935). Since the source of deposit fat in the animal body may be either the fat

contained in the food or the carbohydrate (Lawes & Gilbert, 1859) and protein surplus which may be synthesized to fat (Holmes, 1937), and since the proportion of the former in food used for pig-feeding is limited, the rate of fat deposition may be so great that a considerable proportion of the fat laid down must be synthesized from carbohydrates. This has been demonstrated by Hilditch *et al.* (1939) from a quantitative analysis of the fatty acids of the pigs described in this paper. This leads to an increase in the saturation of the deposited fat because synthesized fat from carbohydrate sources is relatively saturated with an iodine number of 50–60, while the fat formed from oils in the diet is relatively unsaturated (Anderson & Mendel, 1928), usual food oils normally having iodine numbers of over 100. While the "growth-rate theory" can explain the increasing saturation of fat with age and the difference in the iodine numbers of various types of deposit fat, it does not account very clearly for the initial and very significant increase in iodine number in all deposits between birth and 8 weeks. The pig at birth has a fat similar in chemical nature to that of the mother. This is changed from a relatively saturated to a relatively unsaturated fat during the first 2 months. Since the amount of fat laid down during this period is small, it is conceivable that its major source is the milk fat of the mother which would thus require to be highly unsaturated. We have only a limited amount of evidence based on a single sample that this is the case (Callow, 1938). It would be possible if the only source of milk fat was the food fat of the sow. Maynard *et al.* (1936) have demonstrated that unsaturated food fat will increase the iodine number of the milk fat of dairy cows. Since, however, the daily yield of milk fat of the sow is of the order of 0·5 lb. (deduced from data of Roez (1932) and Bonsma & Oosthuizen (1935)), and her daily intake of food fat on a normal ration approximately 50–75 % of this, it would be necessary to postulate extremely high efficiency in the digestion and conversion of food fat to milk fat to ensure that any large proportion of the latter is derived from the former. Moreover the milk fat of other species is not normally of an unsaturated type.

Callow (1938) suggests a possible alternative or associated factor in respect to this initial rise in iodine number. By plotting the fat/tissue ratio against iodine number for different deposits, the resulting curve indicates a relatively greater growth in connective tissue (number of cells) than in the amount of fat (size of fat cell) during the birth to 8-week period. Thereafter the position is reversed. Postulating the existence of two types of fat—"cellular fat", relatively unsaturated and associated

with the metabolism of the cell itself, and "true deposit fat" (the "element constant" and "element variable" of Terroine (1920)) the increase in iodine number could be explained. We have been unable to obtain histological confirmation of hyperplasia in fat cells during post-natal life as assumed here, though this appears likely since it is not evident from histological examination that any marked increase in the size of the fat cell occurs with age.

The relationship between the histological and chemical aspects of intramuscular fat might also be noted. No marbling intramuscular fat could be stained in the new-born pigs nor in the 4-week animals, but the presence of fat was detected as free globules within the muscle bundles at these ages (Pl. 5). On extraction this fat showed a high degree of saturation. As marbling fat appeared at the later ages the iodine number of the extracted fat decreased. Coincident with this situation the free fat globules within the muscles became more difficult to detect until, from 16 weeks onwards, they could no longer be observed. Solution of the many problems arising from these and the aforementioned facts must await more fundamental knowledge of fat metabolism than is available at present.

Table 20. *Changes in iodine number of fat with age*

Age weeks	Internal fat Kidney fat and flares	Subcutaneous fat				Intermuscular fat	
		Back fat		Belly fat			Longissimus dorsi
		Outer layer	Inner layer	Outer layer	Inner layer	Psoas	
Birth	—	58·4*	58·4*	—	—	68·6	71·4
4	65·8	74·2	71·5	72·4	70·9	76·2	72·4
8	69·4	75·1	72·4	73·1	71·6	80·5	75·5
16	59·4	71·0	67·8	70·0	65·7	66·2	64·7
20	55·4	62·1	57·7	61·3	57·2	63·6	57·9
28	53·7	62·9	57·7	62·4	56·2	67·5	59·7

* Inner and outer layers bulked.

Of the fat tissues, the flare fat has the lowest iodine number, and the outer back fat layer the highest. These agree with the results of Henriques & Hansen (1901) but as pointed out by Callow (1935*b*) it is unnecessary to adopt their theory of temperature differences at the seat of deposition being responsible. Differences in the rate of growth explain the position more simply, while in any case the temperature theory no longer fits all the facts. It does not account for the difference in the degree of saturation of the inner layer of subcutaneous and the intramuscular fats, nor will it explain differences in iodine number in different parts of the one tissue.

Thus Callow (1935b) working on our material has shown gradients in iodine number in the back fat and intramuscular fat from head to tail and has correlated these with differences in the local rates of fat deposition. In the younger pigs the iodine number is highest toward the tail region where the rate of fat deposition is low, and lowest at the fore-end where the initial rate is high. This situation tends to be reversed, or the differences reduced for all three tissues at later ages when the rate of fat deposition has shifted in intensity from the fore to the hind end of the body.

It will be recognized that the chemical data in respect to the percentage of fat and its iodine number provide strong confirmation for the existence of differential growth rates in different parts of the body and that the trends suggested are in close agreement with results obtained from the anatomical comparisons.

(11) Summary

1. With the object of establishing the general order of development during post-natal life of the body proportions, tissues, and anatomical units, the relative changes with age in these characters have been studied in a series of male pigs killed at monthly intervals from birth to 7 months. The study is to be regarded in the light of a preliminary investigation, providing a background to experimental studies on the influence of nutrition on the growth and development of the pig.

2. Growth in body proportions, when measured both photographically and by the weight of the individual anatomical regions, conforms to the law of developmental direction, exhibiting a well-defined anterior-posterior gradient from earlier to later developing regions. The limbs appear as relatively early developing parts with the fore limbs slightly earlier developing than the hind.

3. The major body tissues exhibit marked differential growth behaviour: skeleton, muscle, and fat develop in that order. This situation has its origin in the differential rates of growth of the three tissues, in consequence of which the earlier developing skeleton makes a greater proportion of its growth earlier in life than does muscle, while the latter makes a greater proportion of its growth earlier than does the still later developing fat.

4. Within any one tissue, the individual anatomical units or regions of the body similarly show well-defined differential growth relationships. Thus, the skeletal units of the head and trunk exhibit an anterior-posterior gradient in their order of development, while the bones of

each limb show a centripetal gradient, the upper units being later developing than the lower units. To an even more marked degree, both the muscle and the fat surrounding these skeletal units afford evidence of similar gradients in these tissues.

5. The body organs and offals also show marked heterogenic growth. This is such that a functional basis provides an adequate explanation of the differences noted. The parts essential to life processes and body functions appear relatively well developed at birth, and make a smaller proportional amount of growth in post-natal life than the body as a whole. Within these, those organs associated more intimately with growth functions grow proportionately more from birth. Those again whose function is primarily or largely that of storage of nutrient reserves develop little until the later stages of growth.

6. Changes in carcass measurements afford confirmatory evidence for the picture presented above. Relative to the part to which, to a greater or lesser degree, they provide an index, they show the same order in development.

7. Strong supporting evidence for the existence of the gradients described is available from quantitative and qualitative chemical data upon the muscle and fat tissues from different regions of the body.

8. The form as well as the weight of the skeleton is related to body conformation and meat qualities. Differential growth occurs in the bone form as well as in bone weight. The later developing nature of thickness growth as compared with length growth in the bones has been demonstrated.

9. Histological study of age changes in muscle show that increase in the size of the muscle fibre is sufficient to account for the increase in the mass of this tissue. No evidence was obtained of any increase in the number of muscle fibres during post-natal life.

10. The study as a whole reveals the inadequacy of live weight as a measure of growth in the animal body. The growth of the whole is the resultant of differential growth of the constituent parts. Realization of this situation and its implications is important in any study of animal production and fundamental to the study of the meat producing animal.

(To be continued)

APPENDIX I

Breeding of pigs

388 ♂

344 ♀

71 70 69 67 66 23 22 21 19 18 17 13

132 135 131

57 ♂

56 ♀

14 ♂

388 ♂

388 ♂

15 ♀

37 38 50 63 83 84 85 89 34 35 26

78 80 82

95 98 99

72 73 74 100 101 103 106 107

27 35

138 143 139 92 93

22–2

APPENDIX II

Age series—composition of pigs

	Birth		4 weeks		8 weeks	16 weeks		20 weeks		24 weeks			28 weeks
	22 ♂	19 ♂	23 ♂	37 ♂	17 ♂	13 ♂	59 ♀	18 ♂	63 ♀	83 ♂	38 ♀	70 ♂	21 ♂
					Total carcasses (g.)								
Bone	227·7	273·4	694	840	1730	4367	3557	5496	4928	6784	5347	7184	7396
Muscle	324	452	1701	2101	4182	14819	10519	19082	16353	24386	19499	25160	31649
Fat:													
Subcutaneous	32	47	619	914	1660	6056	4278	12831	6817	20470	7357	19242	23845
Intermuscular	10	12	133	252	314	2394	1526	4014	2709	5733	2508	7356	10668
Total	42	59	752	1166	1974	8450	5804	16845	9526	26203	9865	26598	34513
Skin	95	116	351	358	1034	2054	1421	2704	1884	3549	2269	3408	3442
Tendon, glands, etc.	24·7	32·1	152	147	282	861	946	1015	889	1767	1214	1613	1627
Carcass weight	832	1145	3915	4911	10176	31846	23140	45656	34879	63823	39706	65507	80469
					Head (g.)								
Total weight	198	252	623	687	1597	3542	2896	4060	3199	4937	3784	5244	6380
Bones:													
Tongue	0·5	0·7	1·5	1·8	3	7	6	8	9	10	9	9	11
Lower jaw	13·4	15·5	33·0	35·0	87	208	145	245	193	325	234	363	297
Skull	53	65	106	125	287	583	445	772	603	968	642	1056	876
Muscle	13	22·6	54	108	176	674	479	659	659	948	731	960	1016
Fat:													
Subcutaneous	4·9	7·4	87·1	92·0	135	551	489	990	450	785	544	774	1400
Intermuscular	2·6	3·5	35·9	42·7	77	332	169	426	196	369	273	490	922
Tongue	17·8	23·1	35·6	30·3	128	115	102	128	127	135	151	161	198
Brain	35·8	36·8	51·7	49·1	74	101	99	110	99	98	102	101	108
Eyes	3·9	4·0	5·5	5·3	7	10	10	11	10	11	11	11	12
Skin	15	23	50	50	203	210	157	224	157	305	198	256	344
Ears	11	13	55	61	110	221	197	297	255	322	290	335	277
Tendon, etc.	6	7	34	23	35	213	233	264	224	444	252	419	444
Glands	5·8	6·5	49·3	31·4	59	157	255	221	87	222	248	208	317

	Shoulders (2) (g.)												
Total weight	184	268	835	948	2143	6339	4191	7000	6259	11180	7257	11220	13220
Bone:													
Scapula	5·9	9·9	24·7	31·1	65	184	145	232	215	295	228	321	350
Humerus	12·5	19·3	46·5	55·6	113	312	257	380	351	475	378	493	545
Radius-ulna	8·2	13·8	35·4	42·2	84	210	173	260	229	326	248	340	339
Carpals	2·1	3·1	9·9	9·9	19	61	45	64	55	79	63	85	82
Cannons	3·2	5·1	13·5	15·3	26	69	56	79	72	93	78	94	104
Splints	0·8	1·3	3·1	3·9	6	18	14	22	19	29	23	27	34
Dew claws (2)	0·6	1·1	2·8	2·9	6	14	11	18	17	23	18	27	24
Pasterns (2)	1·2	1·8	4·8	5·6	10	27	24	36	31	38	34	44	46
Coronets (2)	0·6	1·0	2·6	3·8	6	16	15	22	19	23	21	27	30
Pedals (2)	0·4	0·7	1·8	1·8	4	9	10	12	12	15	13	16	20
Naviculars and sesamoids (4)	0·5	0·3	1·0	1·1	3	8	6	10	8	9	10	10	12
Muscle:													
Shoulder	77·4	109·6	365	387	922	2872	1926	3343	2944	4489	3503	4711	5528
Arm	13·8	16·3	56	52	117	299	207	382	321	458	394	492	590
Cannon	0·7	0·8	2·6	2·6	6	12	11	15	18	20	21	20	23
Fat:													
Subcutaneous (sh.)	8·0	12·6	126	152	346	1090	580	1469	903	2699	1011	2478	3159
Intermuscular (sh.)	1·5	2·1	17·7	37·2	22	370	224	511	372	855	348	832	1075
Intermuscular (arm)	0·2	0·2	1·5	6·5	5	14	15	85	40	82	53	63	87
Skin	23·2	36·0	81·4	83·6	210	460	257	597	335	641	458	526	739
Tendon, glands, etc.	1·6	5·8	15·9	28·4	63	118	138	133	157	326	181	296	338
	Neck (g.)												
Total weight	59	85	317	410	691	2246	1766	3964	3380	5786	3402	5674	6050
Bone:													
Atlas	1·6	2·4	5·8	6·1	14	41	34	51	48	58	48	60	76
Axis	1·4	2·2	5·3	6·6	13	32	28	40	39	52	39	48	54
Cervical	4·9	7·8	19·4	23·5	49	124	110	164	168	192	156	190	242
Muscle	35	53	166	178	321	1063	890	1683	1430	2170	1680	2064	2476
Fat:													
Subcutaneous	4·3	7·8	68	105	137	412	371	1264	834	2003	870	1803	1451
Intermuscular	0·9	0·6	11	43	65	372	256	444	492	791	352	1024	1345
Skin	3·4	8·0	16·8	18·6	39	56	79	146	161	296	172	282	160
Tendon, glands, etc.	1·7	1·2	9·5	7·8	5	38	28	73	47	84	61	24	28

APPENDIX II (continued)

	Birth		4 weeks		8 weeks	16 weeks		20 weeks		24 weeks			28 weeks
	22 ♂	19 ♂	23 ♀	37 ♀	17 ♀	13 ♂	59 ♂	18 ♂	63 ♀	83 ♂	38 ♀	70 ♂	21 ♂
Thorax (g.)													
Total weight	146	194	853	1167	2356	7104	5617	11546	8573	17252	9757	18251	22639
Bone:													
Ribs and sternum	19·6	32·6	92	105	219	509	440	647	616	865	677	926	1005
Vertebrae	16·6	23·7	68	83	157	388	342	514	529	648	568	659	726
Muscle	66	91	396	522	852	3312	2483	4392	3832	5500	4562	5981	7875
Fat:													
Subcutaneous	3·6	4·6	147	278	496	1548	1320	3663	1996	6439	2145	3687	7216
Intermuscular	1·8	0·9	35	65	85	775	567	1716	1020	2363	978	3534	4838
Skin	24·0	12·3	74	76	222	391	328	676	429	848	568	879	741
Tendon, glands, etc.	1·6	1·4	6	4·4	15	21	11·5	21	14	46	19	15	24
Loin (g.)													
Total weight	48	70	334	426	775	3939	2376	4950	2953	6465	3841	6532	10939
Bone:													
Lumbar vertebrae	7·5	13·2	32	41	96	297	205	339	310	388	320	407	430
Muscle:													
Psoas	5·2	7·6	28	43	58	341	226	414	356	669	350	541	652
Loin	21	32	138	153	282	1503	930	1745	1195	2033	1596	2176	3221
Fat:													
Subcutaneous	3·4	6·7	91	155	191	1093	682	2238	711	3125	912	2791	4740
Intermuscular	0·1	1·3	10	17	18	255	76	196	132	460	116	465	1109
Skin	5·9	6·7	44	43	98	365	198	341	190	512	305	481	575
Tendon, glands, etc.	1·1	1·5	4·6	5·5	10	10	19	14	7	30	46	32	25
Pelvis (g.)													
Total weight	43	64	181	246	469	2120	1742	3791	3344	5953	2939	6426	6461
Bone:													
Pelvis	5·7	11·0	29·4	40·4	82	239	200	330	286	375	313	415	440
Sacrum	2·0	3·4	8·0	10·1	37	65	66	99	78	133	88	122	155
Tail vertebrae	0·4	0·9	1·7	2·1	7	11	14	20	14	22	15	20	25

Muscle	21·3	30·2	96·3	117	219	1035	827	1412	1475	1849	1485	2117	2331
Fat:													
Subcutaneous	1·5	1·5	19·2	47·8	61	472	349	1336	954	2545	655	2869	2473
Intermuscular	0·25	0·5	4·6	14·2	17	73	88	259	209	294	130	342	605
Skin	1·0	2·7	8·5	12	17	36	89	170	192	311	123	340	205
Tendon, glands, etc.	0·6	0·8	3·1	2·4	1·0	36	30	8	17	169	10	90	5
Total weight	154	212	772	1027	2145	6556	4552	9445	7171	12250	8726	12160	14780
Legs (2) (g.)													
Bone:													
Femur	11·5	17·4	50·0	64·7	124	349	285	416	385	499	413	540	571
Tibia-fibula	9·3	14·5	39·7	51·9	89	248	206	305	266	372	316	393	410
Patella	0·7	0·9	2·6	3·6	7	24	17·5	25	22	28	28	33	35
Calcaneum	2·1	3·1	9·1	11·8	20	54	44	67	56	79	63	81	79
Astragalus	2·1	3·3	9·6	13·0	21	56	48	59	53	72	59	75	68
Tarsals	1·4	2·5	6·2	7·1	14	41	32	47	42	55	45	60	60
Cannons	3·3	5·1	13·9	16·7	30	77	62	93	81	102	88	108	104
Splints	0·6	0·9	2·7	3·3	6	14	13	20	16	24	21	26	24
Dew claws (2)	0·6	0·8	1·9	2·4	4	12	9	16	14	21	15	21	19
Pasterns (2)	1·2	1·8	5·0	6·1	10	27	23	39	33	43	35	42	47
Coronets (2)	0·7	1·0	2·7	3·3	6	16	13	23	20	26	21	26	30
Pedals (2)	0·4	0·7	1·6	1·8	4	9	8	15	11	14	12	12	16
Naviculars and sesamoids (4)	0·3	1·0	0·9	0·9	2	8	4·6	7	8	8·2	8·4	8·5	10
Muscle:													
Thigh	57·6	71·1	329	441	920	3164	2098	4191	3458	5257	4290	5085	6738
Leg	12·5	17·1	76	93	180	523	425	815	640	960	855	987	1151
Cannon	0·8	0·9	3·7	4·3	9	31	17	31	25	33	32	26	46
Fat:													
Subcutaneous (thigh)	6·2	6·4	81	134	294	890	487	1871	978	2877	1220	2840	3406
Intermuscular (thigh)	1·9	2·2	12·7	19	20	166	99	308	192	404	198	407	588
Intermuscular (leg)	0·8	0·5	4·5	8·2	5	37	32	69	48	115	60	99	99
Skin	21·7	27·1	70·6	74·2	245	463	322	550	420	636	445	644	685
Tendon, glands, etc.	6·3	7·0	29·4	44·1	94	268	232	281	336	446	397	469	446

APPENDIX II (*continued*)

Organs and offals (g.)

	Birth		4 weeks		8 weeks	16 weeks		20 weeks		24 weeks			28 weeks
	22 ♂	19 ♂	23 ♂	37 ♂	17 ♂	13 ♂	59 ♂	18 ♂	63 ♂	83 ♂	38 ♂	70 ♂	21 ♂
Empty live weight	1142	1532	5437	6424	13209	40750	31454	58500	45619	80960	51137	82429	100000
Blood	124	140	376	391	700	2125	1904	2640	2858	4184	2720	4126	3296
Skin and hair	18	13	100	91	123	483	435	635	561	520	571	505	892
Hoofs, fore	1·5	2·0	3·3	4·7	11	26	19	31	26	47	36	41	56
Hoofs, hind	1·0	1·3	2·8	3·3	6	21	15	25	20	32	30	28	40
Neck thymus	2·4	1·2	6·6	20·5	30	45	31	53	77	159	66	102	84
Heart thymus	1·7	1·8	4·2	6·7	10	43	15	48	33	45	30	38	61
Diaphragm	4·8	8·2	24·5	24·1	53	192	140	254	216	397	226	409	408
Heart	9·0	11·3	49·0	48·0	62	183	147	209	189	307	189	265	266
Pericardium and blood vessels	2·2	2·9	11·8	10·6	20	65	101	62	165	179	126	213	181
Lungs and trachea	17·2	34·4	78·0	98·5	193	463	428	602	503	634	590	656	778
Oesophagus	1·4	1·8	4·3	4·9	15	32	25	43	38	58	53	53	61
Stomach	4·6	7·1	33	45	138	368	372	469	428	615	484	696	574
Small intestine	19·4	24·0	272	166	313	1012	1005	1205	1378	1777	1480	1479	1397
Caecum	0·5	1·2	4·8	5·8	14	81	71	125	102	136	94	139	129
Large intestine	3·3	6·6	24	31	103	427	494	804	641	774	597	727	862
Rectum	2·2	2·8	10·9	14·7	86	175	138	214	100	192	148	253	159
Caul	0·1	0·2	1·4	2·1	3	46	22	66	61	98	70	134	252
Mesentery	5·5	9·0	43·8	31·1	107	416	318	666	521	1006	414	1045	1705
Liver	40·2	52·6	189	190	435	1014	1019	1507	1288	2634	1384	2277	1745
Gall bladder	0·4	0·3	2·1	1·6	12	29	3	28	27	31	33	43	43
Spleen	1·1	1·7	8·1	10·3	21	44	30	58	61	82	50	100	99
Pancreas	1·2	1·9	11·6	17·8	31	93	93	198	61	119	90	121	140
Kidneys (2)	9·0	12·6	41·0	40·8	76	176	164	216	208	490	222	374	225
Leaf and kidney fat	1·1	1·6	14·3	27·1	50	293	183	723	317	1225	262	1524	2295
Bladder	2·5	2·6	2·8	3·1	10	19	15	24	24	49	22	52	50
Penis and vesiculae seminalis	1·8	2·8	15·8	19·8	10	117	127	52	135	96	204	79	39
Total offals and organs	266	256	1323	1290	2623	7990	7314	10957	10038	15886	10191	15479	15837

	Length of alimentary tract (cm.)												
Small intestine	354	348	1210	872	1290	1768	1863	2064	1926	2240	2031	2140	1915
Caecum	3	3	9	8	14	20	18	25	20	23	20	24	23
Large intestine	53	36	113	91	174	203	295	334	318	382	253	336	250
Rectum	18	19	46	40	92	155	113	148	79	117	116	141	159
Total length	428	426	1378	1011	1570	2145	2289	2571	2343	2762	2420	2641	2347
	Carcass measurements (mm.)												
Body length	238	290	401	405	600	896	793	993	950	1045	923	1082	1110
Carcass length	184	194	305	305	345	635	607	695	683	750	650	758	797
Leg length	155	180	252	257	175	491	458	530	520	548	523	570	590
Depth of chest	76	85	123	132	—	265	228	315	263	345	285	350	397
Forearm length	55	64	93	95	—	160	153	200	175	212	180	213	202
Forearm circum.	57	64	102	109	—	178	155	205	180	228	193	232	222
Circum. at base of tail	—	—	33	33	—	—	60	—	68	86	70	78	76
Fore trotter length	36	35	55	49	70	94	92	103	101	92	90	95	106
Belly thickness:													
(1) Breast	3.5	4.0	10.0	13.0	13.0	22	18	24	20	27	22	27	35
(2) Middle	3.0	4.5	10.0	13.0	12.0	22	19	26	19	25	22	25	37
(3) Inguinal	4.0	3.5	10.0	9.0	11.0	23	18	32	20	25	22	25	37
Back fat:													
(1) Shoulder, outer	3	2	4	6	10	10	5	10	10	10	9	10	11
Shoulder, inner	3	2	9	14	16	19	17	31	19	35	19	32	37
(2) Loin, outer	1	1	3	5	4	7	3	10	5	9	4	7	12
Loin, inner	1	1	2	3	3	5	4	13	5	16	6	16	25
(3) Rump (1)	2	2	6	10	11	19	15	34	19	42	17	39	50
Rump (2)	2	1	4	9	8	13	7	24	13	31	14	27	34
Rump (3)	3	2	6	11	11	18	10	30	19	40	23	36	32
Loin cut:													
A	21	27	34	39	57	63	69	72	78	74	87	79	75
B	6.5	6.5	11	12	15	34	24	35	26	36	28	37	49
C	2	2	4	8	8	12	8	25	11	27	11	27	39
H	2	2	6	12	12	18	14	30	15	42	21	40	44
Thickness of skin	1	1	2	2	2	2	2	2	2	2	3	2	3
Muscle colour:													
Diaphragm	2 P	2 P	2 P	2 P	—	3 P	5 P	9 B	—	10 B	6 P	6 P	9 B
Eye at loin	2 P	2 P	2 P	2 P	4 P	—	4 P	3 P	5 P	5 P	2 P	3 P	3 P

P = Pork scale: B = Beef scale (1 = Pale, 10 = Dark).

Fig. 1.

Fig. 2. Changes in size and proportions of skull with age.
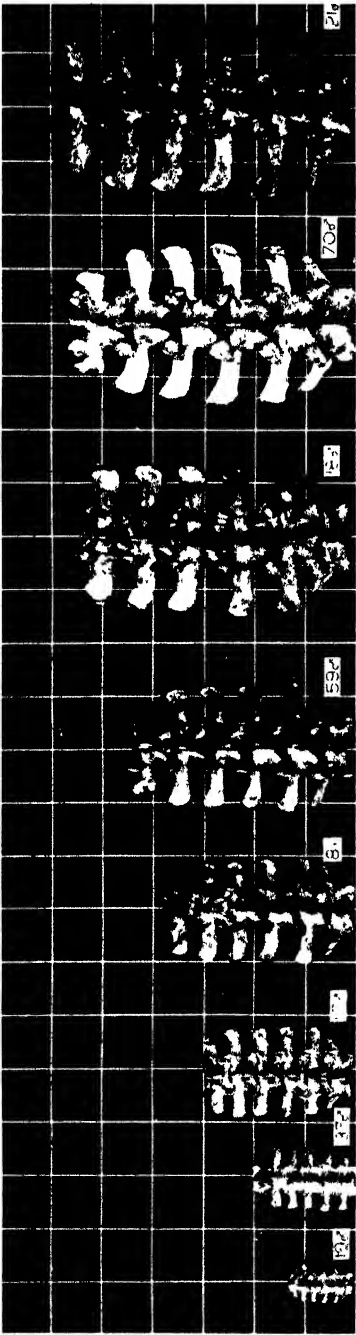
Fig. 1. Changes in size and proportions of lumbar vertebrae with age.
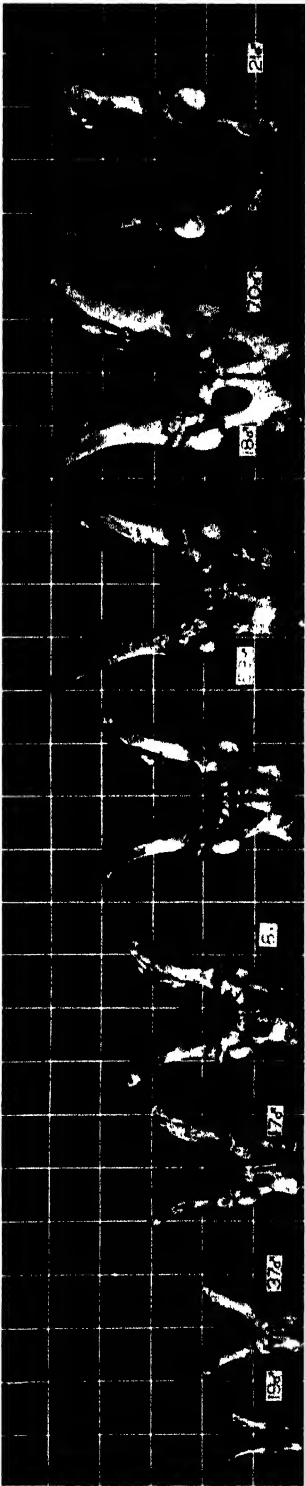
Fig. 2. Changes in size and proportions of pelvis with age.
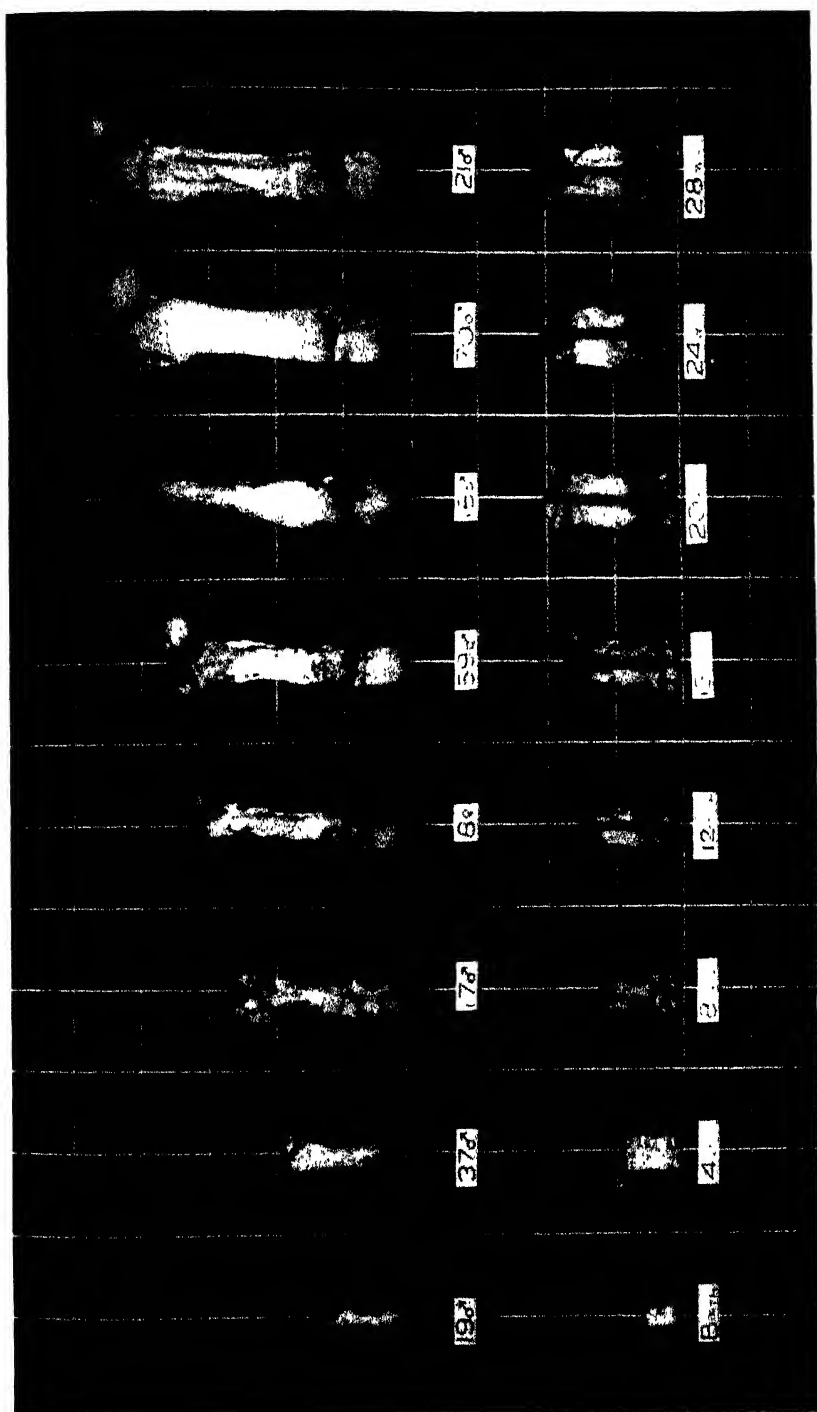
Changes in size and proportions of hind cannons and femur with age.

8 weeks

24 weeks

4 weeks

20 weeks

Birth

16 weeks
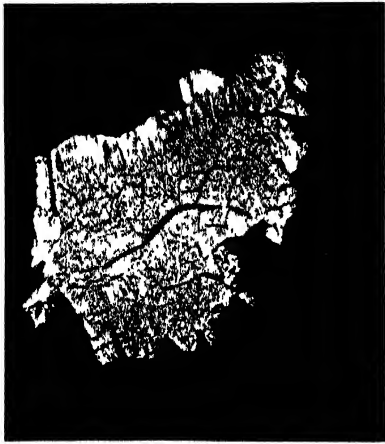
Magnification 3

Sections from eye muscle (longissimus dorsi).

Changes in amount of intramuscular (marbling) fat with age.

Section of longissimus dorsi at 28 weeks. Stained with Sudan III. Note absence of fat in muscle bundles but a large mass of intramuscular fat (stained black) between the bundles.

Section of longissimus dorsi at 4 weeks. Stained with Sudan III. Note aggregates of free fat globules (stained black) within certain muscle bundles.

STUDIES OF SOIL AFTER FIFTY YEARS OF WHEAT OR BARLEY CROPPING, ESPECIALLY OF SOIL MADE ACID WITH SULPHATE OF AMMONIA

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I. INTRODUCTION

IN the year 1876, a series of experiments was commenced at the Woburn Experimental Station, on lines very similar to those which had, even at that time, been going on for many years at Rothamsted. These consisted in growing crops of wheat or barley every year on the same land either without any addition, with various types of fertilizer, or with farmyard manure. The special interest attaching to the Woburn series of experiments was due to the fact that, in contradistinction to the conditions at the much older station at Rothamsted, the soil consists of a light sandy loam, already slightly acid, containing a very small amount of lime. This has led to results which were not anticipated at the time when the experiments were initiated, and they justify a special study of the soils, after the various treatments, at the end of fifty years. Some account of these soils has been given by Crowther (1936), and the present paper may be considered in connexion with his results.

The soil with whose treatment it is proposed to deal in the present studies was derived from the following plots, of which the treatment for the previous fifty years is given:

Plots	Treatment
1	No manuring
2a	Ammonium salts each year (a mixture of sulphate and muriate from 1877 to 1906 and sulphate alone since that time) giving 41 lb. nitrogen per acre from 1877 to 1906 and 20·5 lb. nitrogen per acre from 1907 to 1926
2b	Ammonium salts as on plot 2a, but also with the addition of 2 tons of quicklime per acre in 1897, and an additional 2 tons to the barley land only in 1912
3b	Nitrate of soda each year, giving 41 lb. nitrogen per acre from 1897 to 1906, and 20·5 lb. nitrogen per acre from 1907 to 1926
4 (wheat)	Mineral manures only, consisting of 3½ cwt. superphosphate

Plots	Treatment
4a (barley)	200 lb. sulphate of potash, 100 lb. sulphate of soda, and 100 lb. sulphate of magnesia per acre from 1877 to 1906, and 3 cwt. superphosphate and ¼ cwt. sulphate of potash per acre from 1907 to 1926
5a	Ammonium salts each year, as on plots 2a and 2b and, in addition, mineral manures as on plots 4 (wheat) or 4a (barley)
11b	Farmyard manure, made by cattle, each year, equal to 105 lb. nitrogen per acre from 1877 to 1906, and 82 lb. nitrogen per acre from 1907 to 1926

In all cases no further additions of manures was made after 1926, but the land remained fallow in 1927 and 1928, and then the wheat cropping was resumed without further manuring. It is with the condition of the soils after the end of the fifty years' course of manuring, as described above, that we are dealing in the present paper.

The general character of the soil has been indicated by Crowther (1936). It shows a uniform mechanical composition down to 24 in. deep, after which there is a sudden fall in the silt content and an increase in the coarse sand and stones. The clay fraction shows a high ratio of silica to alumina and a high iron content. There is evidence of podsolization at a former period. The organic matter rapidly decreases with depth. The composition of the soil at the commencement of the experiments is shown by the following analyses, based on extraction with strong hydrochloric acid (Voelcker, 1903).

Table I. *Analyses of soil of Stackyard Field, Woburn*

	1st depth (9 in.) %	2nd depth (9 in.) %
Organic matter and loss on heating	4·13	2·43
(containing nitrogen)	(0·166)	(0·094)
Oxide of iron (Fe_2O_3)	2·93	2·57
Alumina (Al_2O_3)	3·61	2·84
Lime (CaO)	0·31	0·20
Magnesia (MgO)	0·14	0·16
Potash (K_2O)	0·29	0·23
Soda (Na_2O)	0·14	0·22
Phosphoric acid (P_2O_5)	0·16	0·11
Sulphuric acid (SO_3)	0·03	0·02
Insoluble silicates and sand	88·25	91·20
	100·00	100·00

From the beginning, therefore, perhaps the most striking feature of the soil has been its poverty in lime. In samples taken in 1876, the exchangeable calcium has been recently determined by Crowther (1936) as 7·8 mg. equivalents % equal to 0·218 % of CaO.

The effect of fifty years' continuous cropping with either wheat or barley was to reduce the level of yield very greatly on all the plots, while on those treated with sulphate of ammonia without lime (whether with or without mineral manures) the crops almost entirely failed. The actual

average yields of grain for successive periods of years are shown in Table II.

Table II. *Yields of grain per acre on certain wheat and barley plots*

	Wheat				Barley			
Plots	1877–1896 cwt.	1897–1906 cwt.	1907–1916 cwt.	1917–1926 cwt.	1877–1896 cwt.	1897–1906 cwt.	1907–1916 cwt.	1917–1926 cwt.
1	7·62	4·85	5·27	3·64	10·12	5·63	4·80	3·88
2a	12·29	5·01	0·28	0·30	15·61	1·92	0·18	0·75
2b	—	9·38	8·89	4·27	—	10·36	6·93	4·04
3b	11·75	9·47	8·50	7·08	16·40	11·40	7·40	5·33
4	7·82	4·08	4·84	4·42	—	—	—	—
4a	—	—	—	—	10·37	7·93	6·07	4·67
5a	15·86	13·89	8·86	5·06	18·63	3·52	1·37	2·38
11b	14·27	13·46	11·03	9·54	18·69	18·09	14·89	12·26

In all cases, the yield per annum declined greatly, and, at the end of fifty years, the plots showed every sign of being very exhausted, in spite of the annual addition of the appropriate fertilizer for the plot. In the case of the plots treated with sulphate of ammonia, without the concurrent addition of lime, the fertility has almost disappeared and very little yield of either wheat or barley was obtained.

At the end of the fifty-year period, the soils produced were examined for organic matter and nitrogen and also for exchangeable bases by Crowther and his co-workers (1936) and his results are on record. The object of the work now to be described is to examine more in detail the amount of certain water-soluble constituents (calcium, potassium, phosphoric acid, nitrate nitrogen and ammoniacal nitrogen) in the soils resulting from the fifty years of treatment, and then to make a more intensive study of the conditions which are produced in soil when it becomes excessively acid by the continued use of ammonium salts.

II. Aqueous extracts of wheat and barley soils

As a first step to the study of these soils, a series of aqueous extracts of those from the selected plots were made. The samples were taken at monthly intervals during 1929 and to some extent during 1930. They were obtained from the surface to 6 in. deep, and from 6 to 12 in. deep, and were always examined without drying, being weighed out and examined as soon as the sample was taken and mixed. The soils were extracted with water at the ratio of five of water to one of soil, as it has been shown by Hoagland *et al.* (1921) that such extracts give good information as to the relative composition of the soil solution. For the

separation of the soil and extract, where such is necessary, the collodion sac method of Pierre & Parker (1927) was employed, and thus a clear solution was obtained for the determination of lime, potash and phosphate. The amount extracted in 20 hr. was taken as the standard. All the analyses of the extracts were made by well-known methods and, particularly, phosphates were determined by Parker & Fudge's (1927) modification of Denigès's procedure. Nitrate was estimated by phenol-disulphonic acid, and ammonia by distillation with magnesia.

In the first place we may deal with the mean results for soils taken month by month throughout the year 1929. The actual samples numbered eight in each case except with plots 4 (wheat) and 4a (barley) where there were only three, and with plot 5 (barley) where the surface soil only was examined merely on two occasions for phosphates.

Table III. *Analysis of water extracts of soils*

		pH value of soil (1927)	Yield of grain (1929) bush.	Parts per million of air-dried soil				
	Plots			Lime (CaO)	Potash (K_2O)	Phosphoric acid (P_2O_5)	Nitrate nitrogen	Ammonia nitrogen
				Permanent wheat				
1	Surface	5·7	11·1	13·3	15·8	0·2	0·9	3·4
	Subsoil	5·8		13·4	12·0	0·1	0·7	
2a	Surface	4·5	0·3	8·2	15·0	0·2	1·9	4·2
	Subsoil	5·3		11·0	11·8	0·1	1·4	
2b	Surface	5·0	?	12·3	10·3	0·1	1·4	3·5
	Subsoil	5·6		13·4	8·6	0·1	0·9	
3b	Surface	5·8	9·5	14·7	10·0	0·2	1·3	3·1
	Subsoil	6·2		16·3	9·0	0·1	0·9	
4	Surface	5·9	17·8	15·7	24·3	10·0	0·7	?
	Subsoil	6·7		16·3	24·7	5·5	0·8	
11b	Surface	6·4	21·3	11·9	35·5	4·5	1·1	4·6
	Subsoil	6·5		10·7	35·2	2·2	1·2	
				Permanent barley				
1	Surface	5·5	20·4	12·9	14·0	0·1	1·2	2·6
	Subsoil	6·2		13·8	10·8	0·1	0·8	
2a	Surface	4·5	2·7	8·4	19·5	0·3	2·0	5·1
	Subsoil	5·5		9·2	19·0	0·1	1·6	
2b	Surface	5·5	24·9	15·0	12·8	0·3	1·0	4·7
	Subsoil	6·4		16·6	9·3	0·1	0·9	
3b	Surface	5·7	27·2	17·4	11·0	0·2	1·3	3·3
	Subsoil	5·9		14·2	9·0	0·1	0·8	
4a	Surface	6·0	21·1	10·0	16·0	9·8	0·5	?
	Subsoil	6·2		12·0	18·0	3·7	0·5	?
5a	Surface	4·8	5·8	—	—	6·6	—	—
11b	Surface	5·8	34·7	12·4	31·3	6·8	2·1	5·5
	Subsoil	6·0		10·8	36·0	3·1	1·3	

There are two points which strike one immediately in the figures given. The first is the very great similarity between the amounts of water-soluble constituents in the wheat and barley soils, showing that the difference in crop has had little effect on the ultimate condition of the soils used in the experiment. The second point is the very small differences between the top 6 in. of the soil and the second 6 in. It is true that in the more acid soils there has been a tendency for more water-soluble lime to be found in the second depth, while there seems a slight concentration of water-soluble potash in the top layer. But it would be almost satisfactory to use the figures for the top layer of the soil as representing the condition in which the soil has been left at the end of the fifty-year period.

Water-soluble lime. If this is done, we may first consider the results in relation to the amount of *water-soluble lime* in the soils, and compare them with determinations of the exchangeable lime in the same plots at practically the same date by Crowther & Basu (1931). The original amount of lime soluble in hydrochloric acid at the commencement of the experiments in 1876 was (see p. 346) 0·31 % or 3100 parts per million of the air-dried soil. The same soil gave Crowther (1936) the figure of 2184 parts of *exchangeable* lime per million of air-dried soil, or 70·5 % of the total amount extractable by hydrochloric acid. Table IV shows the relationship of the amount of water-soluble lime to the exchangeable lime as given by Crowther.

Table IV. *Relationship of water-soluble lime to exchangeable lime in selected soils*

	Parts per million of surface soil		
Plots	Exchangeable lime (1927) (Crowther) A	Water-soluble lime (1929) B	Percentage of B on A
	Permanent wheat		
1	1372	13·3	0·97
2a	224	8·2	3·66
2b	616	12·3	2·00
3b	1456	14·7	1·01
4	1848	15·7	0·85
11b	1764	11·9	0·67
	Permanent barley		
1	1036	12·9	1·24
2a	252	8·4	3·33
2b	1232	15·0	1·22
3b	1344	17·4	1·30
4a	1400	12·0	0·86
11b	1652	12·4	0·75

The proportion of the exchangeable lime which is soluble in water seems to bear a close relationship to the pH value of the soil, except that, where the land has been manured substantially either with mineral manures (plots 4 and 4a) or with farmyard manure (plot 11b), the proportion of the exchangeable lime which is soluble in water seems substantially diminished. This difference is, however, small in comparison with that which seems to be connected with the pH value of the soil. If we put all plots together which have a pH value of over 5·5, and compare them with those of lower value, we have the results given in Table V.

Table V. *Loss of lime from soils in relation to the changes in pH value*

Plots	pH value of soils in 1927	Exchangeable lime in 1927–9 as percentage of exchangeable lime in original soil in 1876 (Crowther, 1936)	Water-soluble lime in 1927–9 as percentage of exchangeable lime in 1927–9	Water-soluble lime in 1927–9 as percentage of exchangeable lime in original soil in 1876
		Permanent wheat		
1, 3b, 4, 11b	Over 5·5	73·6	0·87	0·64
2b	5·0	28·2	2·00	0·56
2a	4·5	10·3	3·70	0·37
		Permanent barley		
1, 2b, 3b, 4a, 11b	Over 5·5	61·0	1·04	0·64
2a	4·5	11·5	3·33	0·38

It would seem, therefore, that the proportion of the exchangeable lime which is soluble in water is in very large measure a function of the acidity of the soil. The increase in this proportion is not great till the pH value of the soil sinks below 5·5, but, thereafter, it is very rapid, and at a pH value of 4·5 the proportion of lime soluble in water is three times that found at a pH value of 5·5. If this is true, it would seem that the probable loss of lime from an acid soil by drainage increases very much more rapidly than the pH value.

At the same time, it seems clear that there is still a substantial amount of calcium in the water extract from the most acid soil, in spite of the very great reduction in the amount of exchangeable lime. We know, as will be shown later (p. 379), that the calcium in the water extracts from the acid soils is almost exclusively in the form of calcium sulphate or nitrate, and practically not at all in the form of calcium hydrogen carbonate, so that we are faced with the fact that though the reduction in the water-soluble calcium has only been of the order of 30 %, yet the soil has become almost sterile for both wheat and barley.

Water-soluble potash. There is much less information on record as to the effect of manuring on the quantity of available potash in a soil than in the case of lime, but general conclusions as to potash exhaustion have been stated by Crowther (1936) on the basis of exchangeable potash determinations made in 1927. He states that the greatest loss of exchangeable potash was on the less acid plots, while on acidification the loss of base fell almost entirely on the calcium, and there was no evidence that either extreme acidity or liming affected the exchangeable potash.

The following further conclusions can be reached as a result of the determinations of water-soluble potash recorded in Table III. On the plots to which no potash has been added since the beginning of the experiment in 1876, there is no evidence that acidity has led to a reduction of the water-soluble potash. The amount is exactly the same as that in the unmanured plot in the case of the wheat soil, but distinctly greater in the case of the barley soil. This cannot be due to larger crops being taken in the fifty years from the acid plots (2a), as the total produce has actually been less. Plots 2b and 3b yielded a smaller amount of water-soluble potash than the unmanured plot. Taking a mean figure for all the plots which had not received any potash manure during the course of the experiment (12·3 parts potash per million of soil), and comparing the figure for the exchangeable potash as determined by Crowther (calculated to the same units) which is 61 parts per million, we have the water-soluble potash amounting to 20·2 % of the exchangeable potash in the soil. This is an unexpectedly large proportion.

It is to be expected that the amount of water-soluble potash would be very much greater in the case of the plots which had been treated every year with soluble potash salts (in the form of sulphate of potash). The actual amount of such soluble potash which was added in the course of fifty years was 3560 lb. K_2O per acre, which would be equivalent to 1140 parts per million of the air-dry soil 9 in. deep. Seeing that this addition had led to very little increase in the total crop obtained from the land (compare plots 4 or 4a and plot 1 in Table II), it is interesting to see that the increase in the water-soluble and in the exchangeable potash (Crowther, 1936) is so small as a result of the addition. We have only given in Table VI the mean of the wheat and barley soils. The increase in the water-soluble and in the exchangeable potash is remarkably small.

A much larger increase in the water-soluble potash is, however, shown in the plot to which farmyard manure was added during the

whole of the fifty-year period. While there is an increase of 7·6 parts per million in the water-soluble potash as a result of the addition of 3560 lb. K_2O per acre in fifty years, the increase due to the addition of 4100 lb. (approximately) of potash as farmyard manure in the same period is 21·3 parts per million or nearly three times the amount (actually 2·8 times). How far this greater solubility of the potash has to do with the greater maintenance of the fertility for both wheat and barley on the farmyard manure plots, we do not know, but it is an interesting fact that the largest amount of water-soluble potash occurs where there has been continued addition of potash *in the form of organic material*, and on these plots the yield of both crops is best maintained.

Table VI. *Increase in water-soluble or exchangeable potash as a result of potash manuring*

Plots	Water-soluble potash in 1929 A p.p.m.	Exchangeable potash in 1927 B p.p.m.	Proportion of exchangeable potash which is water-soluble %
1	13·1	61·0	21·5
4 or 4a	20·7	117·0	17·7

Water-soluble phosphoric acid. One of the most striking results of the determinations now under discussion is the almost complete disappearance of water-soluble phosphoric acid from the soils to which phosphates have not been applied during the whole history of the experiments. The actual figures recorded are very near the lower limit of determination by the method used, while on those plots to which phosphatic manures or farmyard manure were applied the amount of phosphoric acid is substantial. Yet, at the end of the fifty-year period, there was no markedly greater yield of wheat or barley on the plots to which phosphates had been constantly added (4 or 4a) over that on the plot to which no manure at all had been applied.

On the other hand, after two years' fallow, on soil which is represented by these determinations, there was a very considerable increase of yield in wheat, though a much less marked one with barley (see Table III), on the plots which are shown as giving a larger amount of soluble phosphates. There hardly, however, seems much justification for attributing this increase to the water-soluble phosphate.

There is a certain amount of interest in comparing the amount of water-soluble phosphoric acid found in these soils in 1929 with that readily soluble in slightly acid liquids, as determined by Truog's method (0·002 N sulphuric acid containing a small amount of ammonium sul-

phate) or by 0·5 N acetic acid, in 1927, as reported by Crowther (1936). The actual figures, placed side by side, are as shown in Table VII.

Table VII. *Comparison between amount of water-soluble phosphoric acid and that extracted by dilute acids (mean of wheat and barley soils)*

Plots	Water-soluble P_2O_5 A p.p.m.	Acid-soluble P_2O_5 (Truog) B p.p.m.	A as percentage of B	Acid-soluble P_2O_5 (0·5 N HAc) C p.p.m.	A as percentage of C
1	0·1	25	0·5	10	1·2
2a	0·2	30	0·6	20	0·9
2b (wheat)	0·1	30	0·3	10	1·0
2b (barley)	0·2	40	0·5	10	2·0
3b	0·1	25	0·7	10	1·5
4 (wheat)	7·7	230	3·4	170	4·6
4a (barley)	6·7	190	3·5	120	5·6
5a (barley)	6·6	110	6·0	100	6·6
11b	4·1	110	3·9	70	5·9

There is clearly a very much greater difference between the plots treated with phosphatic manures and those which were not, when extracted with water, than by either of the methods of acid extraction. The difference between the more and the less acid soils seems slight whatever be the method of extraction, and there is no evidence that the more acid plots are more exhausted of soluble phosphoric acid than the less acid plots. If the peculiar effects of the extremely acid plots on the growth of either barley or wheat has anything to do with the absorption of phosphoric acid, it is not a question of there being less in the soil water in the one case than in the other.

Nitrogen as nitrate and as ammonia. In these extremely exhausted soils (except for that which had been treated with farmyard manure) two points seem clear. The first is that the amount of nitrate is very small but differs little in the different soils. The lowness may be due to the fact that the samples were taken at various times during the growth of the wheat and barley crops. This may also account for the relatively high level reached by the nitrate in the plots 2a where the soil is very acid. It is clear, however, that the acidity is no hindrance to nitrification, for the amount of nitrate relative to ammonia is certainly not less than is found in the other less acid plots. The other point of interest is the large amount of ammonia in *all* cases compared with that of nitrate.

III. METHODS OF CORRECTING SOILS TOO
ACID FOR THE GROWTH OF BARLEY

When soil has been treated with sulphate of ammonia for so long as to become infertile for barley, one method, and one only, has in practice been successful in bringing back the lost capacity for growing healthy plants of this crop, namely, the application of substantial amounts of lime either in the form of calcium carbonate or of burnt lime. The question remains, however, unsettled as to whether the recovery of the soils is essentially one of increase in the amount of soluble calcium in the soil or of the neutralization of the acidity caused by the continued addition of sulphate of ammonia. It has, moreover, been suggested that any effect of the acidity may be indirect and be produced by the formation of some poison, possibly soluble aluminium, in the soil, and that if this be got rid of, the soil may again be made to yield healthy plants of barley. It has been possible for us to investigate this matter in the course of the last five years and the results may now be presented.

A. *Effect of increase in the amount of water-soluble calcium in acid soils*

It has already been shown that the failure of the soil of plot 2a to produce healthy crops of barley is accompanied by a fall in its water-soluble as well as in its exchangeable calcium. The question at once arises as to whether, if the water-soluble calcium could be increased to the amount contained in the still fertile plots, wheat or barley could still be grown in a healthy if poor condition. An experiment was consequently laid down to see whether, if soluble calcium salts of different kinds were added to the acid soil from plot 2a (barley) in such an amount as to bring the water-soluble calcium to a figure comparable with or higher than that in the still fertile plots, there would be any appreciable benefit to a barley crop grown on such a soil.

Various salts of calcium were therefore added, in earthenware pots, to the soil from plot 2a (barley) in such proportion as would apparently double, quadruple, or increase by eight times the amount of water-soluble calcium in the soil, and barley was then grown. The salts used were the sulphate, chloride, nitrate, tartrate, and hydroxide of calcium. None of these additions was so large as to raise the pH value of the soil beyond 5·0, but another set of pots was added in which calcium hydroxide was added in eighty times the amount found to be water-soluble in the soil in the field, and this raised the pH value, after the growth of the barley crop, to 5·5.

The growth of the barley plants was closely followed, and their heights were measured just before harvest. After harvest the soil was examined for water-soluble lime, and the whole results are shown in Table VIII.

Table VIII. *Effect of soluble calcium salts on growth of barley on acid soil (from plot 2a, permanent barley)*

Treatment	Ratio of increase of water-soluble calcium added as soluble calcium salts	Height of barley plants at harvest cm.	Water-soluble lime in soil one month after harvest p.p.m.	pH value of soil one month after harvest
1. No addition	—	23·8	18	4·7
2. Calcium sulphate	Twice	25·0	18	5·0
	Four times	23·9	26	4·9
	Eight times	23·9	27	4·8
3. Calcium chloride	Twice	24·2	22	5·0
	Four times	21·9	20	4·8
	Eight times	20·8	40	4·8
4. Calcium nitrate	Twice	22·1	15	4·8
	Four times	23·6	20	4·7
	Eight times	24·8	22	4·8
5. Calcium tartrate	Twice	18·2	15	4·9
	Four times	20·4	17	5·0
	Eight times	22·4	18	4·9
6. Calcium hydroxide	Twice	21·6	15	4·9
	Four times	21·9	20	5·0
	Eight times	26·2	23	5·0
	Eighty times	41·7	29	5·5

Between the time of placing the soil in the pots and the time six months later when the crop of barley had been grown (without, of course, any possibility of drainage away of calcium in any form), the amount of water-soluble calcium has very much increased even in the soil to which no treatment has been applied. At the time when the soil was taken from the field the water-soluble calcium (see Table III) was represented by the figure of 8·4 parts per million of soluble lime. Six months later it contained 18 parts per million, or an increase of 114%. That an increase might be anticipated simply by exposure of the soil to air and moisture was recognized, but that it would take place to the extent indicated was a surprise.

It will also be noticed that the addition of soluble calcium salts has not by any means always led to an increase in the soluble calcium, and that in no case is the increase in soluble calcium as great as the addition made at the beginning of the season. It would seem as if the additions in certain cases had been absorbed into the soil complex without increasing the final amount of water-soluble calcium, and this has happened

specially in those cases (calcium nitrate and tartrate) where the salts added might be expected to be decomposed during the growth of the plants. The increase in the water-soluble calcium is by far the greatest with those salts which would hardly be altered under the conditions of the experiment (calcium sulphate or chloride).

But whatever be the increase in the amount of water-soluble calcium, there has been no marked increase in the size of the stunted plants till an amount of eighty times the original quantity of water-soluble calcium has been added in the form of calcium hydroxide which raises the pH value of the soil to 5·5. In this case the height of the plants was nearly doubled (23·8 to 41·6 cm.) though the amount of water-soluble calcium, reckoned as lime, had only risen from 18 to 29 parts per million.

It would seem, in fact, that the determining factor in making the soil such as will grow normal barley does not lie in the actual proportion of water-soluble calcium.

B. *Effect of application of large amounts of calcium sulphate to acid soils*

The experiment just recorded showed that the addition of small amounts of salts which were calculated to increase the water-soluble calcium in acid soils by anything up to eight times its original value were totally ineffective in bringing back the capacity to grow healthy barley. This does not, of course, show that larger quantities would be ineffective, even of the more stable salts of calcium, and an experiment was therefore carried out to see how far relatively large applications of calcium sulphate would affect the growth of barley on this soil.

The plan of the experiment was as follows: Twenty-seven glazed pots were filled with soil from plot 2a (barley) to which a dressing of potassium phosphate and urea had been added in the previous year. This was

Table IX. *Effect of additions of calcium sulphate and carbonate on crop of barley*

Treat-ments	Applications of calcium salts per pot	Applications of calcium salts per acre	No. of shoots per plant	Total wt. of plants at harvest per pot g.	pH value of soil 24 July
1	None	None	19	0·88	3·8
2	2·43 g. CaSO₄	352 lb. CaSO₄	20	0·67	3·8
3	4·86 ,,	704 ,,	18	0·60	3·8
4	9·72 ,,	1408 ,,	18	0·47	3·8
5	19·44 ,,	2816 ,,	18	0·40	3·8
6	38·88 ,,	5632 ,,	18	0·47	3·8
7	7·14 g. CaCO₃	1046 lb. CaCO₃	54	7·84	4·4
8	14·28 ,,	2092 ,,	108	15·89	5·0
9	28·56 ,,	4184 ,,	137	16·41	5·6

placed in the pots, having been previously mixed with pure calcium sulphate or carbonate as shown in Table IX. With the last portions of the soil urea was added equal to 0·5 g. nitrogen per pot, and potassium phosphate (KH_2PO_4) equal to 0·4 g. phosphoric acid per pot.

Germination was, as usual, not seriously affected in any of the pots, but soon after it became quite evident that none of the applications of calcium sulphate, however large, was going to have any appreciable effect on the failure of the barley. On the other hand, the dressings of calcium carbonate showed themselves in a marked improvement of the plants even with the lowest dressing used. The effect is clearly seen in the number of shoots (tillers) per pot recorded when these were at their maximum on 30 June. These differences continued till harvest, when the whole of the pots to which calcium sulphate had been added gave only pathological plants which bore no ears whatever and did not differ appreciably from those which had had no treatment with calcium salts. The plants grown with calcium carbonate were normal and bigger in size as the addition of this salt became greater. It is clear that the beneficial effect of the calcium carbonate is a specific one and is not merely due to its content of calcium.

As would be expected, the addition of calcium sulphate had no effect on the pH value of the soil, but the application of calcium carbonate had the almost immediate result in raising the latter. The addition of calcium salts was made on 13 April, and the pH value was determined on 24 July of the same year.

The experiment was continued later, so far as the largest dose of calcium sulphate is concerned, together with the several amounts of calcium carbonate. Table X shows the yields of barley plants per pot in

Table X. *Effect of additions of calcium sulphate and carbonate on crop of barley (second, third and fourth years)*

		Total weight of barley plants per pot			pH value of soil			
Treatment per pot		1936 g.	1937 g.	1938 g.	1934	1936	1937	1938
6.	38·88 g. CaSO₄	0·23	0·43	0·20	3·8	4·1	4·0	4·1
7.	7·14 g. CaCO₃	0·97	0·63	0·30	4·4	4·4	4·2	4·5
8.	14·28 „	9·17	2·97	0·47	5·0	4·9	4·8	4·9
9.	28·56 „	11·27	6·60	1·03	5·6	5·4	5·4	5·4

1936 and 1937 and the pH value of the soil in the years succeeding 1934 when the application of calcium salts was made.

It will be seen that the pH value of the soil underwent little change

after the first few months. The results so far as yield is concerned are somewhat curious. The pots treated with calcium sulphate are, as before, only able to grow stunted plants which never have any ears, in fact, they are purely pathological specimens. The smallest dressing of calcium carbonate put on in 1934—when a poor yield was obtained though with more or less normal growth—has, in the two years now being considered, lost its virtue and the plants are equally pathological and almost equally small with those which received the dose of calcium sulphate. This has occurred in spite of the fact that the pH value of the soil has not fallen. The barley produced by the second dressing of calcium carbonate, equal to 10·4 cwt. of lime (CaO) per acre, which gave an excellent growth of normal plants in 1934, became definitely pathological as regards some of the plants in 1936 and completely so in 1937 and 1938, again without material change in the pH value of the soil. So far as the largest dose of calcium carbonate is concerned (equal to 20·8 cwt. CaO per acre) the crop was perfectly normal in 1936, but less so in 1937, for though there was no case of complete breakdown of the plant growth, there were signs that the development was not only poor but was also abnormal. In 1938 the breakdown was almost complete for only two plants out of eighteen succeeded in producing any grain.

It would seen clear, therefore, that there is some factor which determines the failure of the barley plants on these acid soils beyond the mere pH value of the soil. We have previously shown that the primary cause of the plant failure is not the absence of soluble calcium in the soil. It is now equally evident that the failure is not *completely* explained by the acidity as indicated by the pH value determined in mixture with water. We shall have to search further for a complete explanation of the behaviour of the barley plants under the conditions now under investigation.

C. *Effect of application of soluble phosphates to acid soils*

As already stated, on p. 354, it has been suggested (see Magistad, 1925; Hardy, 1926; Pierre *et al.* 1932, 1933) that the primary cause of the failure of barley and other crops on a very acid soil may be due to the development of a poison under these conditions, and that such a poison may be found in the presence of a considerable amount of soluble aluminium. There is no doubt that when the pH value of a soil sinks below a certain point, the amount of aluminium which can be washed out of the soil by water rapidly increases. Our own experiments (see p. 377) indicate that while at any pH value above 4·6 the amount of soluble

alumina removed in the drainage water was fairly constant, yet when the pH value sank to 4·1, this increased to nearly four times the amount. The accumulation of alumina in the ash of the abnormal barley plants grown on acid soil has been shown to occur by one of the authors (Mann, 1937) and this would make the suggestion at least more plausible.

If, however, the failure of the barley plants were primarily due to the presence of abnormal amounts of soluble aluminium in the soil, it would be likely that the addition of any soluble phosphate, and more particularly of a neutral phosphate, would tend to precipitate the soluble aluminium salts and so remove the poison. It seemed, therefore, worth while to test the effect of the application of such soluble phosphates on a crop of barley grown on the soil from plot 2a (barley), which had a pH value of 3·8 at the time of taking the sample. Such an experiment was carried out in 1934. Except in one treatment, the phosphates were added in the form of potassium phosphate (KH_2PO_4) and in the remaining one, as a mixture of one part of calcium triphosphate and two parts of calcium hydrogen phosphate. The general plan of the experiment and the crop obtained are shown in Table XI. Each pot received also 1·07 g. of urea (equal to 0·5 g. nitrogen per pot or 72·5 lb. nitrogen per acre).

Table XI. *Effect of additions of potassium and calcium phosphate on crop of barley*

Treatments	Phosphates added per pot	Phosphoric acid added per acre lb.	No. of shoots per pot (6 plants)	No. of ripe ears per pot	Weight of crop per pot		
					Grain g.	Straw and stubble g.	Total plants g.
1	None	None	6	None	—	0·53	0·53
2	0·4 g. P_2O_5	58	6	None	—	0·63	0·63
3	0·8 ,,	116	6	None	—	0·63	0·63
4	1·6 ,,	232	9	None	—	0·97	0·97
5	3·2 ,,	464	13	5	0·53	2·43	2·96
6	6·4 ,,	928	23	6	2·80	7·83	10·63
7	6·1 g. P_2O_5 as $CaH_4P_2O_8$	884	18	9	5·72	5·03	10·73

The additions made had no effect on the pH value of the soil except in the last-named treatment, where on 24 July, the figure had risen from 3·8 to 4·2.

The additions made, up to treatment 4 (232 lb. phosphoric acid per acre), had no effect on the growth of the barley plants, except that, though equally pathological, they were slightly larger. But they produced no grain, and though a few extra shoots were developed during growth, they all died off before the plants were ripe.

With the next dose of potassium phosphate (treatment 5) a new phenomenon appears. The plants were larger and produced more shoots, though very few of the latter remained till harvest. Moreover, there were a limited number of ears with grains, though an average of only four grains per ear was found. It will be seen that the conditions were still largely pathological.

With the largest dressing of potassium phosphate (treatment 6) the plants were again bigger, had a larger number of shoots, and ripened a slightly larger number of grains, yet the usual purpling of the stalks and leaves, which prevails in all these abnormal plants, still occurred to a slight extent. In addition, a new form of unhealthiness showed itself in a yellowing of the leaves with brown spots and patches.

On the addition of calcium phosphate in large amount (treatment 7) we have the most healthy plants of the series, but there was still a good deal of the usual purpling of the leaves while, later on, the yellowing and spottiness of the leaves just described also appeared. The same soil sown at the same time, after treatment with 16 g. of lime (CaO) per pot in the form of calcium carbonate gave a yield of 5·72 g. grain, 10·17 g. straw and stubble, and so a total weight of 15·89 g. of air-dried plants.

It will thus be seen that, judged by the actual yield of grain obtained, the highest dose of potassium phosphate, with the very large amount of 6·4 g. of phosphoric acid per pot (928 lb. P_2O_5 per acre) is only able to give half the yield of grain which is obtained by the use of 16 g. of lime per pot, while the total product is only two-thirds the amount. A better result is obtained using calcium phosphate containing a slightly smaller amount of phosphoric acid. All smaller amounts than these seem to be very largely or entirely ineffective.

At the same time, it is clear that whatever be the cause of the partial efficiency of the phosphate treatment, it is not directly due to a reduction in acidity, for the pH value of the soil in the most extreme case still remains at 4·2, which is already far below the critical point for the growth of healthy barley in this soil.

We are thus led to the point when neither a deficiency of calcium, nor a mere too great acidity, nor the presence of soluble alumina would seem *by itself* to account for the incapacity of the acid soil to grow healthy barley, though all together they might possibly achieve this result. It was, at this point, suggested that if some colloid buffering agent could be introduced into the soil without lowering the acidity to below the critical point, it might be possible to grow healthy barley on this soil. Some sort of organic matter seemed to be the most likely agent for achieving this

purpose, and it was decided to investigate the effect of treatment with large doses of farmyard manure.

D. *Effect of application of large doses of farmyard manure*

Soil which had refused to grow anything but tiny pathological plants of barley, and which had a pH value of 4·4, was taken and filled into pots after mixing with an amount of farmyard manure equivalent to a dressing of 10, 20, 40, and 80 tons respectively of wet farmyard manure per acre. The material was mixed with the whole of the soil in the pot (namely 39 lb.) in the dry condition, it having been dried without heating to more than 60° C.

The details of the applications and of the resulting changes in the pH value of the soil are shown below:

Treatment	Wet farmyard manure per acre tons	Dried farmyard manure per pot g.	Mean 1936	6 August 1937	22 April 1938
			pH value of the soil	
1	None	None	4·2	4·3	4·5
2	10	38·7	4·5	4·6	4·7
3	20	77·3	4·7	4·8	4·9
4	40	154·7	5·0	5·1	5·1
5	80	309·8	5·3	5·3	5·4

The farmyard manure was mixed with the soil on 4 April 1936, and the barley was sown three days later. During the first year, and in fact throughout the experiment, the pH value of the soil was below the critical point for the healthy growth of barley in all but the last two treatments.

In all cases germination was quite successful, and ten plants were finally left in each pot. Those in the pots without any addition from the beginning were of the same tiny, pathological kind which is customary on this acid soil. But it was evident that the results would be entirely different even in the pots which received the lowest amount of farmyard

Table XII. *Effect of farmyard manure on crop of barley in acid soil (first year)*

Farmyard manure added tons per acre	Shoots per plant (maximum)	Ears per plant	Grain g.	Straw, etc. g.	Total produce g.
			Yield of produce per pot	
None	1·0	0	0·1	1·2	1·3
10 (wet)	4·5	2·8	22·8	25·9	48·7
20 ,,	6·7	3·2	26·7	27·1	53·8
40 ,,	7·6	3·8	28·1	33·5	61·6
80 ,,	10·0	3·3	23·6	60·8	84·4

manure, while the luxuriance increased progressively with the addition of larger amounts of this material. Table XII shows some of the details of the growth of the plants with each treatment.

✓ The largest amount of farmyard manure was, apparently, too great for a normal development of the barley, which, in spite of being perfectly healthy, developed rather to tillers and straw than to grain, as has so often been found with excessive quantities of farmyard manure. But the real interest of these figures is to show that by the addition of an amount of organic material, represented in this case by farmyard manure, which does not decrease the acidity to below what is usually the pathological level, a perfectly normal and healthy growth has been obtained.

This is still more shown by the behaviour of the plants during growth, for, except for a slight purpling of the lower stalk in a few cases, they remained healthy and luxuriant at all stages, even with the lowest dressing of farmyard manure, in spite of a pH value of the soil of 4·5 during the 1936 season.

It was an interesting matter to see how far this effect of the farmyard manure would continue, and so barley was again grown in these pots in 1937 and in 1938. The results are shown in Table XIII.

Table XIII. *Effect of farmyard manure on crop of barley
in acid soil (second and third years)*

	1937			1938		
		Yield of produce per pot			Yield of produce per pot	
Farmyard manure added tons per acre	Ears per plant	Grain g.	Total g.	Ears per plant	Grain g.	Total g.
None	0	Nil	2·4	0	Nil	0·4
10 (wet)	1·0	2·4	6·9	0	Nil	0·6
20 ,,	2·0	5·3	10·5	0·5	0·25	1·8
40 ,,	3·0	7·7	14·1	2·0	6·9	18·4
80 ,,	Lost	Lost	Lost	3·0	9·1	21·1

In spite of the obvious decline in luxuriance, the plants with the lowest dressing of farmyard manure (pH 4·6) were still strong and produced normal ears in 1937, but collapsed completely in 1938. The yield on the next higher addition of manure became very small in 1938 though the highest two doses still yielded healthy plants. In 1939, only the highest dressing of farmyard manure gave reasonably normal growth, and it is evident that the effect of the manure is gradually passing off, even though there has been only a very slight change in the pH value of the soil.

IV. THE EFFECT OF LIME ON SOILS ALREADY MADE
ACID WITH AMMONIUM SALTS

It is evident that the soil that has been made acid by treatment with ammonium salts for a period of fifty years, and which has, in consequence, become unable to grow anything but stunted barley plants which are almost a pathological curiosity, affords a very interesting problem in the study of soil generally. It seemed, in fact, worth while to take such soil, to treat it with variable amounts of lime (which is known to cause a recovery of its capacity to grow wheat or barley) and then continue the treatment with ammonium salts, and at the same time with sodium nitrate. If this be done, and if the crops of barley be weighed and examined, and if, also, the drainage water from the soil under such conditions be analysed, it would be likely to give light on two important matters, namely, (1) the question of the nutrition of barley on soils of varying but high acidity, and (2) the effect of varying acidity on the loss of valuable constituents by drainage.

In order to carry out this programme pots were filled in the spring of 1933 with the soil from plot 2a (barley) after adding quantities of calcium carbonate (10, 20, 30 and 40 g. $CaCO_3$ respectively) corresponding to about 1, 2, 3 and 4 tons of lime (CaO) per acre, mixed with the soil to 18 in. deep, and also with phosphate of potash in sufficient amount (0·77 g. per pot) to ensure the presence of an adequate supply of phosphates and potash. Then, to some of the pots, rather large applications of ammonium sulphate or sodium nitrate were given, and repeated for six successive years. The additions of calcium carbonate were made as pure precipitated material and those of phosphate as potassium phosphate (KH_2PO_4) in solution.

The additions of calcium carbonate were made once for all; those of potassium phosphate were made in the first, second and fourth years of the experiment, being mixed in the later years, however, only with the top 6 in. of the soil; the additions of ammonium sulphate or sodium nitrate were made in solution, each year. The dressings of the nitrogenous salts were large, and each of them really amount to 244 lb. of nitrogen per acre, equivalent to 1153 lb. (10·3 cwt.) per acre of sulphate of ammonia or 1485 lb. (13·3 cwt.) per acre of nitrate of soda. The application of these large amounts should cause more rapid changes in the soil than have been obtained in the field, but are well within the quantities which can be applied without danger to the crop of barley.

After each crop of barley in the first four years (and twice during the

first year), the soil was carefully leached with 2500 c.c. of water per 30 lb. of soil, and the amount of soluble nitrogen compounds, as well as of the bases and acids in the drainage water, were determined. Apart from this leaching there was practically no drainage from the pots at any time of the year.

Let us see what happened to the soil and crop under these circumstances. We start with a soil already made very acid (pH 4·0) by continued treatment in the field with ammonium salts, but this acidity has now been partly neutralized with calcium carbonate. We will consider various criteria of the effect of the treatment.

A. pH *value of the soil.* As already stated, the pH value of the soil (taken in water) before calcium carbonate was added and the experiment begun was 4·0, and thus it was so acid as to grow only very stunted plants of barley. Further determinations at some time in the year after each successive application of nitrogenous manures are shown in Table XIV.

Table XIV. *Effect on pH value of soil of applications of calcium carbonate and other materials*

Treatment g. CaCO₃	First year (Oct. 1933)	Second year (mean of 5 tests)	Third year (mean of 2 tests)	Fourth year (June 1936)	Fifth year (Aug. 1937)	Sixth year (March 1938)
No nitrogenous manure						
10	4·8	4·6	4·7	4·6	4·5	4·7
20	5·0	5·2	5·0	4·9	4·8	5·0
30	6·0	5·3	5·3	5·3	5·2	5·3
40	6·4	6·0	5·6	5·6	5·6	5·6
0·5 g. nitrogen as sulphate of ammonia, every year, per pot						
10	4·7	4·1	3·7	3·4	3·3	3·4
20	5·0	4·6	4·0	3·6	3·3	3·5
30	6·2	5·0	4·5	4·1	3·4	3·6
40	6·3	5·3	4·9	4·4	3·5	3·7
0·5 g. nitrogen as nitrate of soda, every year, per pot						
10	4·8	4·7	4·7	4·7	4·8	5·0
20	5·6	5·2	5·2	5·0	5·2	5·3
30	6·1	5·5	5·5	5·4	5·5	5·6
40	6·4	6·0	5·7	5·8	5·9	5·8

From these figures it is clear that when a soil has become as acid as this one, it does not recover its basicity by standing and working. This is interesting because in the earlier stages of the Woburn experiments, in 1902, when the acidified soil was exposed to the air for a winter, it became quite capable of growing a barley crop again (Voelcker, 1903). This has not been the case in the field since 1926, in the course of ten years during which no further acidifying manure like sulphate of ammonia has been added, and there is no sign of its taking place in the present figures. In the absence of any further addition of ammonium

salts, the pH value of the soil has little changed since the first year except with the larger amounts of calcium carbonate. This is also the case when sodium nitrate is added each year, even in large amount.

B. *Character of the crops of barley.* It has been shown (Part III) that the barley crop will grow healthily up to a point of acidity in the soil which we have called the "critical point", and which seemed, in the present soil, to be about a pH of 4·7–5·0. It would, therefore, appear that there should be no difficulty in maintaining a normal barley crop in most of the above cases, provided there is sufficient plant food present. Where no nitrogenous manure is given we should expect a gradual falling off of the crop, but with sodium nitrate the yield should not fall off. The actual results in the quantity of total produce grown per pot in five successive years is shown in Table XV.

Table XV. *Effect on yield of barley on acid soil of applications of calcium carbonate and other materials*

Weight of total produce of barley per pot

Treatment g. CaCO$_3$	1933 g.	1934 g.	1935 g.	1936 g.	1937 g.	1938 g.
			No nitrogenous manures			
10	16·0	10·9	11·8	16·2	9·6	1·6
20	25·5	11·1	13·3	21·1	12·5	4·3
30	28·5	15·7	13·8	19·9	14·3	6·0
40	35·4	17·9	14·9	19·3	13·9	8·5
	0·5 g. nitrogen per pot every year, as ammonium sulphate					
10	15·5	1·6	0·5	0·2	0·05	0·1
20	35·8	24·0	7·1	0·6	0·1	0·2
30	43·0	31·1	24·3	17·1	0·2	0·3
40	44·5	33·9	26·6	28·7	8·3	0·4
	0·5 g. nitrogen per pot every year, as sodium nitrate					
10	31·9	29·2	29·6	30·0	18·1	11·1
20	41·2	31·6	31·5	31·5	17·2	9·8
30	37·9	29·7	27·0	30·5	20·1	25·1
40	43·0	32·7	29·9	26·5	18·8	30·5

From this set of figures the following results emerge:

(1) So long as the pH value of the soil remains above 5·0 or thereabouts, and there is an adequate allowance of nitrogenous manure, the yield of barley is remarkably constant in each year.

(2) When the pH value is higher than 5·0, further additions of lime, in presence of adequate nitrogenous manuring, did not further increase the yield of barley in the earlier years. This is a rather surprising result, though it agrees with the field records, where additional lime, after a certain pH value has been reached, has not given an increase in barley yield.

(3) If no nitrogenous manure is added the result is slightly different. Here there is, at any rate in the early years of the experiment, a regular increase of yield as the amount of lime added becomes greater.

(4) Once the acidity of the soil exceeds the critical point, the yield rapidly declines, but not regularly. At a certain stage there is complete collapse and only stunted pathological plants result.

(5) When the soil approaches the limit of acidity for the normal growth of barley, the plants take on a peculiar colour, the green being much darker than normal with a waxy sheen. They look, in fact, as if they were growing in presence of an excess of nitrogenous manure.

C. *Composition of the crops of barley.* We have only followed the composition of the crop obtained on these acid soils in a part of the series, but for the first year we have records of the changes in the ash content and the silica contained in the ash, and, for several years, of the difference in nitrogen content caused by the several treatments.

As far as the grain is concerned, the amount of the ash is hardly altered by the varying quantities of lime added to the originally acid soil, nor by the presence or absence of nitrogenous manure. The grain grown on the more acid soils, however, contains more silica in the ash. This is, of course, exactly the result obtained by one of us (Mann, 1937) when examining plants and crops obtained in the field. In the cases of extreme acidity there is always an increase of nitrogen in the grain, perhaps because proper ripening does not take place. Otherwise, there

Table XVI. *Effect on the ash, silica, and nitrogen content of barley grain, of applications of calcium carbonate and other materials*

	1st year			2nd year	3rd year	4th year
Treatment g. CaCO$_3$	Ash in grain %	Silica in grain %	Nitrogen in grain %	nitrogen in grain %	nitrogen in grain %	nitrogen in grain %
			No nitrogenous manure			
10	2·43	0·31	1·83	1·88	1·79	1·71
20	2·33	0·30	1·57	1·98	1·79	1·30
30	2·17	0·27	1·55	1·58	1·69	1·34
40	1·94	0·17	1·54	1·56	1·80	1·38
		0·5 g. nitrogen as ammonium sulphate per pot				
10	1·84	0·20	2·72	No crop	No crop	No crop
20	1·88	0·14	2·14	2·48	3·29	No crop
30	1·83	0·14	1·96	2·23	2·70	2·86
40	1·76	0·09	2·28	2·16	2·94	2·75
		0·5 g. nitrogen as sodium nitrate per pot				
10	1·71	0·20	1·77	2·09	2·50	2·80
20	1·73	0·15	1·60	2·16	2·40	2·42
30	1·83	0·17	1·99	2·42	2·48	2·72
40	1·84	0·12	2·12	2·45	2·61	2·79

does not seem much connexion between the acidity, within the limits when normal growth is possible, and the nitrogenous content of the grain. Even in these acid soils, however, the addition of a nitrogenous manure in the quantity used means a very large increase in the nitrogen content of the grain.

Within the degree of acidity of these soils in the first year of the experiment, the composition of the straw and stubble was affected in the same way as the grain so far as the amount of silica was concerned. Increase in the amount of calcium carbonate added, with the consequent decrease in the acidity, caused a reduction in the percentage of silica in the ash. As regards the nitrogen content of the straw, this would appear to remain constant, for any particular supply of nitrogen, as long as the pH value of the soil remains above about 4·7. When it is more acid than this, that is to say, whenever the conditions prevent the formation of a normal plant, the nitrogen in the straw immediately rises, sometimes to very high levels, as in the soil treated with ammonium sulphate in the third and fourth years of the series.

Table XVII. *Effect on the ash, silica, and nitrogen content of barley straw, of applications of calcium carbonate and other materials*

Treatment g. CaCO$_3$	1st year Ash in straw	1st year Silica in straw	1st year Nitrogen in straw	2nd year nitrogen in straw	3rd year nitrogen in straw	4th year nitrogen in straw
			No nitrogenous manure			
10	5·42	1·76	0·58	0·49	0·63	0·47
20	5·39	1·88	0·43	0·68	0·92	0·36
30	5·09	1·63	0·55	0·49	0·62	0·40
40	5·09	1·10	0·44	0·40	0·79	0·44
		0·5 g. nitrogen as ammonium sulphate per pot				
10	4·74	1·40	1·29	1·47	2·60	2·08
20	4·66	1·06	0·83	0·91	1·74	2·40
30	4·86	0·86	0·70	0·78	1·10	1·58
40	4·86	0·86	0·88	0·69	1·22	0·99
		0·5 g. nitrogen as sodium nitrate per pot				
10	4·40	1·14	0·54	0·70	1·01	0·90
20	4·28	0·95	0·58	0·70	1·02	0·71
30	4·38	0·74	0·70	0·69	1·03	0·84
40	4·59	0·62	0·70	0·77	1·09	1·06

Whenever the soil is not too acid to produce a normally grown crop (and even in some cases where there is already too much acidity for normal growth), the effect of the nitrogenous manuring is apparent either in an increased growth or in an increased amount of nitrogen in the crop. The actual recovery of nitrogen in the crop, i.e. in the corn, straw, or stubble, as a result of adding 0·5 g. nitrogen per pot, is as shown in Table XVIII.

Table XVIII. *Percentage of nitrogen added which is recovered in plants*

Treatment g. CaCO₃	1933 %	1934 %	1935 %	1936 %
	0·5 g. nitrogen as ammonium sulphate per pot			
10	15·0	(−18·0)	(−20·8)	(−26·8)
20	41·6	45·4	(− 0·8)	(− 0·6)
30	44·2	40·6	42·0	30·8
40	55·2	48·8	47·6	49·2
	0·5 g. nitrogen as sodium nitrate per pot			
10	33·2	44·8	52·6	52·0
20	35·6	50·0	51·6	42·4
30	34·6	46·4	44·4	51·6
40	42·6	51·8	52·6	56·8

The recovery of the nitrogen added, with the two salts used, commences at an acidity which is considerably greater than that at which what may be called a normal growth is obtained. Apart from one or two exceptional cases, the nitrogen recovery appears to be almost the same at all stages of acidity represented by a pH value higher than 4·8. The mean recovery of nitrogen from ammonium sulphate is 40·0 % and from sodium nitrate 46·4 % of the amount added. In the first year after the addition of calcium carbonate, the recovery with sodium nitrate is considerably less than with ammonium sulphate, but later in the experiment the position is rather reversed. In no case, even up to the greatest acidity, have we found evidence that the nitrification of the ammonia is prevented.

D. *Composition of the drainage waters.* During the growth of the barley crops in these pots, no drainage of water was allowed, but after harvest the soils were leached carefully by a technique described elsewhere, so that any readily soluble matter in the soil, whether derived from or caused by the original applications of lime or by those of nitrogenous manure, or existing in the original very acid soil, can be determined. The object was to ascertain (1) the rapidity with which the added lime could be washed out of such a soil, and the form in which it appears in the drainage waters, (2) the extent to which other mineral constituents of the soil are found in the drainage water and whether the addition of large amounts of lime led to the greater or less loss of these constituents, (3) the extent to which the added nitrogen not used by the crops can be found in the drainage water and in what form it appears there.

The leaching of the soil was done as follows:

(1) 12 October 1933, after the first crop of barley.

(2) 22 February 1934, before the second crop of barley. (These two leachings were made between the first and second crops of barley.)

(3) 18 October 1934, after the second crop of barley.

(4) 17 September 1935, after the third crop of barley.

(5) 5 January 1937, after the fourth crop of barley.

Generally speaking, the method used was as follows: 2500 c.c. of distilled water were used for each pot, put on in five lots of 500 c.c. each, at intervals of several hours. The pots were then left until they ceased to drain, the leachates being measured, bottled and preserved with toluene to prevent any changes in the composition of the liquids.

The actual volume of drainage obtained from the addition of equal amounts of water to the soil decreases with increased application of calcium carbonate. This occurs whether no nitrogenous manure.is added, or whether the addition is in the form of ammonium sulphate or of sodium nitrate. Taking the whole of the five leachings noted above, the relative amounts of drainage obtained for every litre of water obtained with the smallest addition of calcium carbonate is shown in Table XIX.

Table XIX. *Effect of calcium carbonate in reducing drainage from soils*

Treatment g. $CaCO_3$	No nitrogenous manure c.c	Ammonium sulphate c.c.	Sodium nitrate c.c.
10	1000	1000	1000
20	1035	900	985
30	944	881	932
40	951	850	834

The effect of the lime in retaining water in the soil was greatest with the soil treated with sulphate of ammonia and least where no nitrogenous manure at all had been added. The absolute quantity of drainage water was least with the soil treated with nitrate of soda and greatest with that to which no nitrogenous manure had been applied.

The effect of calcium carbonate in increasing the retaining capacity of soil for water may be a not unimportant element in the value of a lime dressing of an acid soil.

Nitrogen content of drainage waters

The analysis of these leachates with respect to their nitrogen content, taken in conjunction with the determination nitrogen in the crop removed, enables us to determine the amount of nitrogen which an unmanured but limed soil of this acid character is able to render available in a succession of years, and also to ascertain how far the recovery of nitrogen added either as ammonium sulphate or as sodium nitrate takes

place under the circumstances. Table XX shows the amount of nitrogen recovered in these two ways (plants grown and drainage waters taken together) in four years, namely, from 1933 to 1936.

Table XX. *Total recovery of nitrogen (plants and drainage) from acid soils with varying amounts of calcium carbonate*

Treatment g. CaCO₃	1st year nitrogen recovered per pot mg.	2nd year nitrogen recovered per pot mg.	3rd year nitrogen recovered per pot mg.	4th year nitrogen recovered per pot mg.	Mean for 4 years mg.
			No nitrogenous manure		
10	250	150	141	171	178
20	320	236	225	191	243
30	349	197	205	213	241
40	405	208	204	231	262
		0·5 g. nitrogen as ammonium sulphate per pot			
10	402	172*	286*	279*	285
20	503	369	238	377*	372
30	561	377	364	350	413
40	696	436	419	416	492
		0·5 g. nitrogen as sodium nitrate per pot			
10	428	392	429	457	426
20	486	406	473	400	441
30	519	414	431	437	450
40	616	465	406	480	492

* Plants not normal.

The first point brought out by these figures is that the recovery of nitrogen, whether originally present in the soil or added as nitrogenous manures, tends to rise as the amount of lime added to the acid soil is increased and, consequently, the acidity is reduced. This is the case where the crop is normal as well as where it is poor. The gradation is, however, entirely caused by the differences in crop, and the drainage water does not show any such effect. The most curious point, in fact, is that the *drainage water from the pots which have received nitrogenous manure in the same year before the crop of barley was grown, do not show any greater content of nitrogen in the drainage water than those where no such manures were applied,* provided the crops were of a normal and not of a pathological character. The crops may be counted as reasonably normal in all but the first two lots of the sulphate of ammonia application.

The result just noted seems so important that it may be well to set out the recovery of nitrogen by leaching separately for each year of the experiment. These figures are given in Table XXI.

The proportion of the nitrogen added in the nitrogenous manures which can be recovered in either the crop or the drainage water taken

Table XXI. *Recovery of nitrogen in drainage from acid soils with varying amounts of calcium carbonate*

mg. nitrogen per pot

Treatment g. CaCO$_3$	1st year	2nd year	3rd year	4th year	Total
		No nitrogenous manure			
10	89	24	27	36	176
20	108	132	97	69	396
30	90	62	85	93	330
40	102	66	56	108	332
		0·5 g. nitrogen as ammonium sulphate per pot			
10	166·5	152	275·5	275	869
20	82·5	37·5	114	252	486
30	81·5	38·5	33·5	75·5	229
40	113·5	49·5	32	47	247
		0·5 g. nitrogen as sodium nitrate per pot			
10	101	58	51·5	61·5	272
20	86	52	87	66	301
30	87	46·5	88·5	59	281
40	100	64	52	74	290

after harvest is, taking the four years together, not widely variable where the growth of the plants was reasonably normal. But it is much smaller than would be expected with soluble manures like those employed. Table XXII shows the actual position. In each case the amount recovered is obtained after the addition of 500 mg. nitrogen in one form or the other, while the total for the four years is obtained after the addition of 2000 mg. The percentage of nitrogen recoverable in crop and drainage water together is not widely different in these acid soils treated with lime from that which we have obtained in normal soils of the same class. Where sodium nitrate has been used as the source of nitrogen, the mean recovery is 45·0 % and there is no regular gradation

Table XXII. *Amount of nitrogen added which is recovered in plants and in drainage waters*

Treatment g. CaCO$_3$	1933 mg.	1934 mg.	1935 mg.	1936 mg.	Total weight mg.	Total proportion of amount added %
		0·5 g. nitrogen as ammonium sulphate per pot				
10	152	22	145	108	427	21·3
20	183	133	13	186	515	25·7
30	212	180	159	137	688	34·4
40	291	228	215	185	919	45·9
		0·5 g. nitrogen as sodium nitrate per pot				
10	178	242	288	286	994	49·7
20	166	170	248	209	793	39·6
30	170	217	226	224	837	41·8
40	211	257	260	249	977	48·8

in the amount with the addition of varying amounts of calcium carbonate. With the largest amount of lime the addition of ammonium sulphate has given a very similar figure (45·9 %).

The form of the nitrogen in the drainage waters is nitrate almost entirely, and nitrification seems quite possible in all soils used in this experiment. Table XXIII shows the amount of nitrogen as ammonia relative to the amount present as nitrate in the drainage water from each soil in each year.

Table XXIII. *Percentage of total nitrogen in drainage water which is in the form of ammonia*

Treatment g. CaCO$_3$	1933 %	1934 %	1935 %	1936 %	Mean %
		No nitrogenous manure			
10	1·4	2·9	6·0	3·6	2·9
20	1·0	1·6	2·2	3·3	1·6
30	1·2	0·5	2·7	2·4	1·7
40	1·2	1·7	2·4	2·5	1·9
		0·5 g. nitrogen as ammonium sulphate per pot			
10	1·3	1·9	1·7	2·4	1·8
20	1·9	4·2	1·6	1·2	2·2
30	1·8	6·3	7·6	3·4	4·8
40	1·1	3·2	5·6	3·5	3·4
		0·5 g. nitrogen as sodium nitrate per pot			
10	1·2	3·3	3·1	2·7	2·6
20	1·4	5·4	2·5	2·9	3·0
30	1·6	5·4	2·9	3·7	3·9
40	1·2	3·7	4·2	2·6	2·9

Though the figures given are very irregular, they show that the extreme acidity of the soils treated with ammonium sulphate is no bar to the almost complete conversion of the added ammonia into nitrate, and that decreasing acidity does not make this conversion any more complete. This is in conflict with results obtained elsewhere (Hall, Miller & Gimingham, 1908) but it agrees with other experiments which we have made with these very acid soils. The amount of nitrogen as nitrite was negligible in all the cases where this was determined.

Bases present in drainage waters

One of the main objects of the present series of experiments was to ascertain the rapidity with which the added lime could be washed out of such an acid soil, and how far this was affected by the actual dressing made. It was also desired to see the extent to which other bases were washed out and how their loss was affected by the addition of calcium carbonate in various amounts.

For the purpose in view, it will be well at first to consider the total of each of the bases removed from the soil during the five leachings indicated on p. 368. The amounts have been calculated for an equal amount of drainage water and are given as milligrams per litre, i.e. as parts per million (Table XXIV).

Table XXIV. *Bases in drainage water from acid soils (parts per million)*

Treatment g. CaCO₃	Lime (CaO)	(Parts per million) Soda (Na₂O)	Potash* (K₂O)	Magnesia† (MgO)	Nitrogen as ammonia
		No nitrogenous manure			
10	57·2	8·0	18·4	7·1	0·7
20	141·0	9·3	23·6	11·2	1·1
30	151·1	9·1	21·2	12·0	0·8
40	168·6	8·9	14·8	8·8	1·0
		0·5 g. nitrogen as ammonium sulphate per pot			
10	285·9	10·7	46·4	38·7	2·4
20	248·5	10·1	21·6	21·6	1·3
30	207·4	8·8	15·1	12·3	1·6
40	248·9	8·2	13·2	12·4	1·3
		0·5 g. nitrogen as sodium nitrate per pot			
10	36·3	86·2	10·8	8·7	1·1
20	54·3	91·8	9·2	10·2	1·3
30	62·8	90·4	10·0	7·7	1·5
40	95·4	101·0	9·1	5·9	1·4

* Four leachings only.   † Two leachings only.

Lime in drainage water. The effect of the addition of ammonium sulphate has been almost to double (1·9) the amount of lime leached from the soil per unit of drainage, while the addition of a similar amount of nitrogen as sodium nitrate has been to halve (0·48) it. The result has been of the same order in each of the leachings, and shows the great effect of sodium nitrate as an economizer of lime; at least in such an acid soil as we are dealing with. The additions of ammonium sulphate have, as would be expected, largely increased the loss of lime in every case, and, here, the loss of lime per unit of drainage has tended to increase as the soil has become progressively more acid. Thus, in the fourth year after the addition of ammonium sulphate in four successive years, when the pH value has been brought from 5·6 to 3·9, the lime in the drainage water was almost doubled (1·91) per litre.

The amount of lime washed out from the soil increases with the amount of lime added where sodium nitrate is used or where there is no addition of nitrogenous manures, but there is no such increase where ammonium sulphate is used. Table XXV shows this.

The loss of lime from this soil by drainage, as a result of the addition

of ammonium sulphate is not greater when the dose of lime added is increased, a point of considerable importance in deciding the best method of reclamation of such acid soil. On the other hand, either where no nitrogenous manure is added or where it is added in the form of sodium nitrate, the lime drained out increases with the amount of lime applied, at least up to an addition of four tons per acre.

Table XXV. *Relationship of lime drained away*
to amount of lime added to soil

Amount lime added tons per acre	No nitrogenous manure		Ammonium sulphate		Sodium nitrate	
	Lime in drainage units	Mean pH	Lime in drainage unit	Mean pH	Lime in drainage units	Mean pH
1	1	4·7	1	4·0	1	4·7
2	2·5	5·0	0·9	4·3	1·5	5·2
3	2·6	5·5	0·7	4·9	1·7	5·6
4	2·9	5·9	0·9	5·2	2·6	6·0

The units are based on the amount of lime drained with the smallest addition of lime in each case.

The effect of the use of the nitrogenous manures in question on the loss of lime per acre by drainage is also revealed by these experiments. The actual amount of nitrogen added in the course of four years was 976 lb. per acre in both cases. The loss or the saving of lime by such additions is shown in Table XXVI. The figures given represent the excess or deficiency of CaO in the leachate over that with no nitrogenous manure.

Table XXVI. *Increase or decrease of loss of lime by drainage*
due to addition of nitrogenous manures

Amount lime added per acre tons	Sulphate of ammonia		Nitrate of soda	
	Total drainage of lime per acre lb.	Loss lime per lb. nitrogen added lb.	Total drainage of lime per acre lb.	Loss lime per lb. nitrogen added lb.
1	+385·6	+0·40	− 31·6	−0·032
2	+144·9	+0·15	−143·6	−0·147
3	+ 81·6	+0·084	−128·9	−0·132
4	+100·1	+0·103	−124·1	−0·127

The figures given show the actual effect on the loss of lime due to the nitrogenous manure, that is to say, they show the excess or deficiency in the lime drained away over that which was yielded by the soil without any addition of nitrogenous manures. They indicate, therefore, that with ammonium sulphate, after a very great loss amounting to 0·4 lb. of lime for every pound of nitrogen added with the smallest addition of lime,

the amount drained away falls to a much smaller figure with the larger amounts varying from 0·08 to 0·15 lb. of lime per pound of added nitrogen. With sodium nitrate, the effect is always to cause a saving of lime, small (0·032 lb. per pound of nitrogen added) while the soil remains at a mean pH value of 4·7, but much larger (0·13–0·15 lb. of lime per one pound of added nitrogen) when the pH value has been raised to the higher figures of 5·2–6·0.

If the loss of lime continued at the same rate, after application of ammonium sulphate, as in these experiments, the length of time before the soil would be again reduced to the condition in which it was when these experiments were started would be very great, amounting to 135 years for an annual addition of 200 lb. ammonium sulphate per acre, 67½ years for an annual addition of 400 lb., and 44 years for an addition of 600 lb.

These figures partially account for one feature of the Permanent Barley experiments at Woburn which has always been rather difficult to explain. On plot 2*b*, when the barley began to fail as a result of the application of sulphate of ammonia about 1898, 2 tons of lime per acre were added and the dressing was repeated in 1912. In spite of the continued application of sulphate of ammonia in the thirty years up to 1926, first at the rate of 41 lb. of nitrogen per acre each year till 1906 and thereafter at the rate of 20·5 lb. nitrogen per acre, the crop, though poor, continued to be of a normal character totally unlike that grown on plot 2*a* where no lime had been added. From Table XXVI it would seem that it is probable that it would go on producing normal crops of barley, *so far as the loss of lime is concerned*, for a very long time.

Soda in drainage water. Reverting to Table XXIV, we may now consider the loss of the soda by drainage from this acid soil, and, apart from the soda added in the nitrate of soda itself, it seems as if its loss from the soil by drainage is almost independent of the amount of lime added, of the pH value of the soil, and even of the addition of ammonium sulphate. What is more, the amount extracted in successive leachings is at least of the same order. This is a rather remarkable result, especially in view of the results on the loss of potash by drainage, now about to be considered.

Potash in drainage water. Basing his statements on examination of samples of the soil at the beginning and at the end of fifty years of the Woburn experiments, Crowther (1936) wrote that the "greatest loss of exchangeable potassium was on the less acid plots, upon which relatively large crops were grown without added potash. On acidification the loss

of base fell almost entirely on the calcium, and there is no evidence that either extreme acidity or liming affected the exchangeable potassium."

The evidence which we now present tells a rather different story. If we turn again to Table XXIV, it will be seen that the loss of potash by leaching from this very acid soil, however treated, is very considerable and is a very substantial proportion of the amount of lime leached under similar conditions. The actual relationship of the amount of the two bases is shown by the figures in Table XXVII, it being assumed that the proportion is the same in the first leaching (when the potash was not determined) as in the remainder.

Table XXVII. *Proportion of potash to lime in drainage water*

Treatment with lime per acre tons CaO	Potash as percentage of lime extracted		
	No nitrogenous manure	Ammonium sulphate	Sodium nitrate
1	32·2	16·2	29·8
2	16 7	8·7	16·9
3	14·0	7·3	15·9
4	8·8	5·3	9·5

These figures show what a large loss of potash, relative to the lime, by drainage may occur in such acid soils as these. In all cases the proportion becomes lower as more and more lime is added, even when we are dealing with the most acid of these soils. The proportion is lowest in the soils treated with ammonium sulphate, while it is strikingly similar in the other two cases.

In absolute amount, the loss of potash by drainage is by no means small. Table XXVIII shows the amount of potash removed by drainage of 60 in. of water. This is probably about the amount which would drain through such a soil in the course of four years.

Table XXVIII. *Loss of potash (lb. per acre) by drainage per acre from 60 in. drainage water*

Treatment with lime per acre tons CaO	No nitrogenous manure	Ammonium sulphate	Nitrate of soda
1	60·5	147·2	33·3
2	74·7	69·6	29·4
3	67·9	46·8	30·1
4	46·7	40·1	26·7

The loss of potash by drainage is, therefore, much more substantial than would have been thought. In every case, the application of increasing amounts of calcium carbonate has led to a progressive decrease

in the amount of potash lost. There is, moreover, a remarkable saving of potash due to the application of sodium nitrate, noticeable at every rate of addition of calcium carbonate. With ammonium sulphate, there is also a slight saving, except with the smallest addition of calcium carbonate, where the highest point in loss of lime is reached. The figures make it probable that, in the complete absence of any addition of calcium carbonate and with the continued application of ammonium sulphate, the loss of potash by drainage may reach very high figures.

Magnesia in drainage water. The determination of magnesia in the drainage water was only undertaken in connexion with the last two leachings and, hence, the data are not so numerous or complete as in the other cases. The amount of magnesia in the drainage water, however, decreases with the amount of calcium carbonate added to the soil, and the absolute amount of magnesia leached from the soil is reduced in all cases by the application of sodium nitrate. The highest amount of magnesia is found in the drainage water from the pots treated with ammonium sulphate and particularly from the more acid of these pots.

The proportion of magnesia to lime varies a good deal with the several treatments. The more acid of the pots give a larger proportion of magnesia to lime than the less acid ones which have been treated with a larger amount of calcium carbonate. Curiously, the proportion reaches its highest point with the smallest dressing of lime followed by the application of sodium nitrate. It seems clear that the use of sodium nitrate affects the mechanism for the extraction of magnesia less than it does that of lime.

Ammonia in drainage water. The amount of ammonia found in the drainage water is little affected by the treatments except in one case. This is the most acid of the pots treated with ammonium sulphate where the amount of ammonia found is clearly higher in practically all cases than with any other treatment.

Alumina in drainage water. There is always a trace of aluminium in the clear leachates from these pots, and in one of the leachings (the third, in 1934) the amount was determined, with the results shown in Table XXIX.

Table XXIX. *Alumina in drainage water*

Treatment with lime per pot g. $CaCO_3$	No nitrogenous manure p.p.m.	Ammonium sulphate p.p.m.	Sodium nitrate p.p.m.
10	0·4	1·9	0·4
20	0·5	0·5	0·4
30	0·6	0·8	0·4
40	0·5	0·4	0·4

It will be seen that, although the amount of alumina is measurable, it is so small that its inclusion would make no appreciable difference to the balance of acids and bases in the drainage waters. On the other hand, it is quite clear that when the soils reach a higher stage of acidity, the amount of alumina in the drainage water increases and the only case where the alumina reaches more than 1 part per million is where the pH value of the soil is about 4·1.

Acids present in drainage waters

Although the soils from which the drainage waters are obtained are all acid (though of very different acidities), the pH value of the drainage waters obtained as described above varies much less than would have been expected. The figures on which this statement is based are shown in Table XXX.

Table XXX. *Acidities of drainage water from acid soils*

Treatment with lime per acre tons CaO	No nitrogenous manure		Ammonium sulphate		Sodium nitrate	
	pH value of soil	pH value of leachate	pH value of soil	pH value of leachate	pH value of soil	pH value of leachate
1	4·7	5·6	4·0	5·2	4·7	5·7
2	5·0	5·7	4·3	5·5	5·2	5·7
3	5·5	5·5	4·9	5·5	5·6	5·8
4	5·9	5·7	5·2	5·8	6·0	5·8

The differences in the pH value of the leachates are very small compared with the differences in the soils themselves. The determinations were all done by the colorimetric method and using the same test colouring matters. Altogether, they show a liquid slightly acid but in no case greatly so.

It was quite evident, at once, that the greater part of the acid radicles contained in these drainage waters were those of sulphuric and nitric acids. The former is there in large quantity in all cases because the soil has been treated for over fifty years with sulphate of ammonia, the latter because nitrification seems quite active in these soils and any base available would naturally be taken up by the nitric acid formed. These, with a small amount (in most cases though not in all) of bicarbonate, almost constituted the whole of the acid radicles determined. The amount of phosphoric acid was determined in one leaching, and an attempt was made to determine the silicic acid in another. These two last acid radicles will be discussed separately.

The amounts of the three principal acid radicles contained in the drainage waters are shown in Table XXXI. This represents the result for the whole of the five leachings taken together.

Table XXXI. *Acids in drainage water from acid soils*

Treatment per pot g. CaCO$_3$	Nitrate (N) p.p.m.	Sulphuric acid (SO$_3$) p.p.m.	CO$_2$ as HCO$_3$ p.p.m.
	No nitrogenous manure		
10	20·6	65·0	0·8
20	46·6	115·0	1·6
30	41·5	122·6	1·9
40	41·4	140·4	4·2
	0·5 g. nitrogen as ammonium sulphate per pot		
10	96·3	210·0	−2·1
20	60·0	220·6	−0·8
30	28·2	250·2	0·8
40	31·3	310·3	3·9
	0·5 g. nitrogen as sodium nitrate per pot		
10	31·8	86·0	1·3
20	35·6	101·5	1·9
30	35·0	104·9	2·8
40	37·7	134·7	3·7

The bases are clearly in no case, except to a very small extent, leached as carbonate. They appear chiefly as nitrate and sulphate and the amount of these acids present is almost equivalent, as we shall show later, to what is required to neutralize them. The amount of nitrate present in the drainage water is, of course, dependent very largely on the success of the crop of barley which was grown previous to each of these leachings. The amount of sulphate is sensibly the same with no manure and with nitrate of soda, but, as would be expected, the amount is much increased with the addition of ammonium sulphate.

Two other acids appear in the leachates, namely, phosphoric acid and silicic acid. Only one set of determinations of the phosphoric acid was made, namely, in the last leaching of the series. The amount of this acid found in the drainage water in each case was exceedingly small, as Table XXXII shows.

Table XXXII. *Phosphoric acid (parts per million) in drainage water from acid soils*

Treatment per pot g. CaCO$_3$	No nitrogenous manure	Ammonium sulphate	Sodium nitrate
10	0·1	0·1	0·3
20	0·1	0·1	0·2
30	0·2	0·1	0·2
40	0·1	0·0	0·3

The soils used in this experiment are definitely very deficient in phosphoric acid, as is shown by the analyses quoted on p. 348, but

and yet the quantities obtained in the drainage waters are so minute as to be practically negligible. The loss of phosphoric acid from these very acid soils is definitely not the result of leaching into the drainage or into the subsoil.

It was quickly evident, in the course of these experiments, that a certain small amount of silica in the form of soluble silicates occurred in all the drainage waters. But owing to the extreme difficulty in getting the leachates in an absolutely clear condition, its determination represented a difficult problem. Certain of the drainage waters, chiefly the more acid ones, ultimately became crystal clear and could be used for the purpose. Those to which much lime had been added were more difficult to clear, and yet if the merest trace of clay material remained in the drainage water, the values obtained for the silicic acid would be entirely misleading. An attempt was, however, made in the fifth leaching to determine the silicates by throwing down the colloidal matter by means of a trace of alum, filtering, and determining the silica in the filtrate. The results are shown in Table XXXIII. The figures in italics are those which were obtained by using leachates cleared with alum.

Table XXXIII. *Dissolved silicic acid (parts per million)*
in drainage water from acid soils

Treatment per pot g. $CaCO_3$	No nitrogenous manure	Ammonium sulphate	Sodium nitrate
10	14·1	29·8	14·5
20	*19·8 (?)	22·3	*12·8*
30	*12·3*	21·5	*10·4*
40	*16·1*	15·9	*12·9*

* Solution not quite clear.

It will be seen that the amount of soluble silicates appearing in the drainage waters is fairly constant except when the acidity greatly increases. The soils which have received ammonium sulphate and are hence more acid than any of the others give a much larger amount of leached silica than the others.

Mineral balance sheet

How far do the bases which have been determined account for the amount of the several acids which have been found in the drainage waters? This question has been before us during the whole of the present experiments, and it was quickly found that there was a general correspondence though usually a slight excess of the basic radicles. It is only,

however, in the last leaching that the determinations that have been made have enabled us to survey the position completely in this respect, and it is only the figures for this leaching that are now presented. The results, for this purpose, have been calculated as milligram-equivalents per pot, so as to make the comparison simpler. Table XXXIV shows the results.

Table XXXIV. *Mineral balance sheet for drainage waters*

Bases (mg.-equiv. per pot)

Treatment per pot g. CaCO$_3$	Lime (CaO)	Soda (Na$_2$O)	Potash (K$_2$O)	Magnesia (MgO)	Ammonia (NH$_3$)	Total bases per pot
			No nitrogenous manure			
10	4·99	0·57	1·00	0·91	0·08	7·55
20	9·55	0·54	0·71	1·10	0·16	12·06
30	12·50	0·57	0·63	1·21	0·16	15·07
40	14·73	0·60	0·59	1·43	0·19	17·54
		0·5 g. nitrogen as ammonium sulphate per pot				
10	27·75	0·92	2·98	4·63	0·46	36·74
20	31·35	0·83	1·07	2·55	0·21	36·01
30	18·20	0·55	0·38	1·42	0·19	20·74
40	19·00	0·59	0·33	1·19	0·12	21·23
		0·5 g. nitrogen as sodium nitrate per pot				
10	2·35	6·24	0·37	0·96	0·12	10·04
20	3·03	6·95	0·36	1·20	0·14	11·68
30	2·96	6·33	0·39	0·94	0·16	10·78
40	5·27	7·14	0·28	0·62	0·14	13·45

Acids (mg.-equiv. per pot)

Treatment per pot g. CaCO$_3$	Nitrate (N$_2$O$_5$)	Sulphate (SO$_3$)	Bicarbonate	Silicate (SiO$_2$)	Total acids per pot	Difference bases − acids
			No nitrogenous manure			
10	2·50	3·79	0·03	0·83	7·15	0·40
20	4·78	6·31	0·07	(1·27?)	12·43	− 0·37
30	6·50	6·84	0·07	1·10	14·51	0·56
40	7·58	8·21	0·06	1·03	16·88	0·66
		0·5 g. nitrogen as ammonium sulphate per pot				
10	19·22	15·50	− 0·09	2·04	36·67	− 0·07
20	17·80	16·20	0·00	1·57	35·57	0·44
30	5·22	14·80	0·10	1·33	21·45	− 0·71
40	3·28	17·21	0·08	0·90	21·47	− 0·24
		0·5 g. nitrogen as sodium nitrate per pot				
10	4·28	4·66	0·06	0·83	9·83	0·21
20	4·57	5·57	0·05	0·80	10·99	0·69
30	4·07	5·04	0·06	0·63	9·80	0·98
40	5·15	5·92	0·07	0·67	11·81	1·64

It will be seen that the correspondence between the bases and acids, while close, shows, in practically all cases, except where ammonium sulphate has been used, an excess of bases in the drainage water, while it would have been expected that the excess would be the other way.

In other words, it seems as if some of the bases have been extracted in the form of salts of some acid which has not been estimated. The only clue to the nature of this acid is the fact that the residue after evaporation of the drainage water, in practically every case, chars slightly on heating, and hence there would appear to be some form of organic matter present.

One of the earliest observations in connexion with the soils at Woburn under annual treatment with sulphate of ammonia is that such soil appears to lose organic matter rapidly and the plots in the field show a soil appreciably lighter in colour than the rest of the area under Permanent Barley. It is more than possible that the excess of bases in the drainage waters from these acid soils may be in the form of salts of organic soil acids.

V. Summary

A. *Aqueous extracts of wheat and barley soils*

1. Monthly aqueous extracts of soils which have been under wheat and barley cropping on the Woburn light sandy loam soils, with various manuring show very great similarity in the amount and character of the materials extracted in the wheat and the barley soils.

2. Water-soluble phosphoric acid and potash are in extremely small amount where these manures have not been applied during the fifty years' treatment, but, in spite of this, the amount of these constituents does not appear to be a limiting factor in determining the yield of either wheat or barley. The phosphoric acid is much higher in the plots treated with phosphatic manures, and the potash is slightly higher in those treated with potash manures, but these facts do not seem to have secured a seriously higher yield.

3. Nitrogen in the soluble form, whether as nitrate or as ammonia, has become almost completely exhausted after two years' fallow following the fifty years' cropping with wheat or barley. In the most acid soil nitrification seems to be as vigorous as in any of the others.

4. Though the water-soluble lime is considerably less in the soils which have become acid as a result of treatment with sulphate of ammonia, yet, in the light of experiments made with the addition of neutral calcium salts, it does not appear that the absence of water-soluble calcium is the main cause of the complete stunting of the barley grown on these soils.

B. *The correction of soils too acid for the growth of barley*

1. There is evidence that while the increase in the acidity of the soil due to the continued application of sulphate of ammonia to this soil is primarily responsible for the collapse of the growth of barley, it is not the only factor in determining whether the plants will or will not grow. Other things remaining the same, there appears to be a critical amount of acidity above which it is impossible to produce healthy plants, but this critical point can be altered by various treatments of the soil. For instance, by the application of large doses of soluble phosphates, even if these be purely neutral and do not affect the pH value, very much improved barley plants can be obtained, though in no case was perfectly normal growth secured. This suggests that a part of the collapse of the barley plants is due to some poisonous constituent of the soil which can be precipitated by means of a large excess of a soluble phosphate, and, in view of other work, it is suggested that this poisonous constituent may be soluble aluminium.

2. Small additions of calcium salts, calculated to increase the water-soluble calcium in the soil, have had no effect, and even large additions of calcium in the form of calcium sulphate have proved equally ineffective. But, judging by the fact that calcium phosphate is rather more effective in correcting the condition of the soil than an equal quantity of phosphoric acid added as potassium phosphate, it appears that the addition of calcium in a suitable form has some, though only a minor, effect on the recovery of the barley plants. This is rather confirmed by attempts to neutralize the soil with other materials than lime and calcium carbonate, for these have not been successful in making it healthy for barley growing (Voelcker—unpublished).

3. Successful and normal barley plants can be grown on acid soil with an acidity substantially greater than the critical point, if only organic matter be added, at any rate if this latter is in the form of farmyard manure. Even a dressing of ten tons per acre of farmyard manure, which only raised the pH value of the soil fractionally—that is to say to a pH value of 4·5—was quite capable of giving normal barley growth, and a larger quantity than this removed all trace of the characters which mark barley grown on acid soil. The effect gradually disappeared in succeeding years, commencing with the smaller amounts used, when the barley tended again to produce only the pathological specimens of plants to which we have become accustomed on soils with the pH value in question. Whether the effect of the farmyard manure was

due to any particular constituent or to a buffering action which prevented the acidity from having its full effect is not yet clear, but it is evident that the correction of toxicity due to acidity in soils is a new use for the coarser organic manures of which farmyard manure may be taken as a type.

C. *The effect of lime on the crops and drainage waters of soils made acid with sulphate of ammonia*

1. When a soil which is extremely acid as a result of the continued application of sulphate of ammonia is treated with calcium carbonate, the pH value rises rapidly to a point at which good growth of barley is again possible. Apart from the further addition of sulphate of ammonia, the acidity has altered little more in the course of six years with annual cropping with barley. This is the case both without nitrogenous manure and with the addition of sodium nitrate.

2. So long as the pH value of the soil remains above 5·0 or thereabouts, and there is an adequate allowance of nitrogenous manure, the yield of barley remains fairly constant. Further additions of calcium carbonate beyond the amount required to give the above pH value did not increase the yield of barley, provided the amount of nitrogenous manure used is adequate.

3. Once the pH value of the soil is lower than the critical point (i.e. when the acidity is greater than this), the yield rapidly declines, but not regularly. At a certain stage there is complete collapse and practically no growth. When the soil approaches the limit of acidity for the normal growth of barley, the plants take on a peculiar colour, the green being much darker than normal with a waxy sheen.

4. The addition of calcium carbonate to the very acid soils used (pH 4·2) tends to increase the capacity of the soil to retain water. This happens whether the soil is unmanured or whether it is treated with dressings of ammonium sulphate or sodium nitrate.

5. Extreme acidity of the soil, even that equivalent to a pH value of 3·5, is no bar to nitrification.

6. Where growth of barley plants is normal, about 40 % of the nitrogen added as ammonium sulphate or sodium nitrate can be recovered in the plants and drainage waters in the first year. The drainage was always taken after the reaping of the crop of barley. Under these circumstances, and with a dressing of 244 lb. nitrogen per acre in either of the forms named, it was not possible to extract a larger amount of nitrogen in the drainage water than from a similar soil to which no

nitrogenous manure had been added. Where the growth of the barley was not normal, a much larger amount of nitrogen could be extracted by drainage.

7. The addition of sodium nitrate in the amounts just specified led to a reduction of the loss of lime by drainage by about half, while the addition of an equivalent amount of ammonium sulphate doubled it.

8. When the dressing of calcium carbonate is increased, on a soil whose original acidity is represented by a pH value of 4·0–4·2, the amount of lime contained in the drainage water increases in the cases where no nitrogenous manure is applied or where sodium nitrate is used. Where ammonium sulphate is employed, the loss of lime by drainage did not increase with the quantity of calcium carbonate added, possibly because the drainage water was carrying all the calcium possible even with the lowest addition of lime.

9. The amount of soda removed by drainage from this acid soil was almost independent of the amount of calcium carbonate applied, of the pH value of the soil, or of the addition of ammonium sulphate.

10. The leaching of potash from an acid soil like the present is much greater than has been generally thought. Application of increasing amounts of calcium carbonate leads to progressive decrease in the amount of potash in the drainage water. There is a great reduction in the potash that can be drained away where sodium nitrate is applied to the soil, and the same is true when ammonium sulphate is used, except where the acidity is extreme.

11. The more acid the soil, the higher the proportion of magnesia in the drainage water in relation to the lime. The use of sodium nitrate only slightly affects the relative amount of lime and magnesia in the drainage water.

12. The amount of alumina in the drainage waters from these acid soils remains almost constant till the pH value is below 4·6, but at pH 4·1 there is a great increase to nearly four times the previous amount. The total quantity of alumina in the drainage waters is, however, in all cases very small. At a pH value of 4·1, the alumina in the drainage water was only 1·9 parts per million, against a normal amount of 0·4 to 0·6 part per million in the less acid soils.

13. The acid radicles in the leachates from these very acid soils treated with calcium carbonate are almost exclusively nitrate and sulphate. In certain cases there is apparently a small amount of bicarbonate, but even in the most acid soils there is practically no phosphate. When the pH value of the soil is above 4·0 there is an almost constant

amount of dissolved silicate in the drainage water: when the pH value went down to 3·3, the proportion of silicic acid was doubled.

14. With these acid soils, the bases determined are in almost all cases slightly in excess of the amount needed to neutralize the acids determined. This suggests that a small amount of the bases is attached to and leached as a salt of soil organic acids.

REFERENCES

CROWTHER, E. M. (1932). *J. roy. agric. Soc.* **93**, 199. (Summary.)
—— (1936). In E. J. Russell and J. A. Voelcker, *Fifty Years of Field Experiments at the Woburn Experimental Station*, Part IV, p. 315.
CROWTHER, E. M. & BASU, J. K. (1931). *J. agric. Sci.* **21**, 689.
HALL, E. D., MILLER, N. H. J. & GIMINGHAM, C. T. (1908). *Proc. roy. Soc.* B, **80**, 196.
HARDY, G. (1926). *J. agric. Sci.* **16**, 616.
HOAGLAND, D. R., MARTIN, J. C. & STEWART, G. R. (1921). *J. agric. Res.* **20**, 381.
LIGON, W. S. & PIERRE, W. H. (1932). *Soil Sci.* **34**, 307.
MAGISTAD, O. C. (1925). *Soil Sci.* **20**, 18.
MANN, H. H. (1937). *J. agric. Sci.* **27**, 108.
PARKER, F. W. & FUDGE, J. F. (1927). *Soil Sci.* **24**, 109.
PIERRE, W. H. & PARKER, F. W. (1927). *Soil Sci.* **23**, 13.
PIERRE, W. H., POHLMAN G. G. & McILVAINE, T. C. (1932). *Soil Sci.* **34**, 145.
PIERRE, W. H. & STUART, A. D. (1933). *Soil Sci.* **36**, 211.
POHLMAN, G. G. (1933). *Soil Sci.* **36**, 47.
VOELCKER, J. A. (1903). *J. roy. agric. Soc.* **64**, 357.
—— (1923). *J. roy. agric. Soc.* **84**. 115. (Summary.)

GROWTH AND DEVELOPMENT IN THE PIG, WITH SPECIAL REFERENCE TO CARCASS QUALITY CHARACTERS

PART II. THE INFLUENCE OF THE PLANE OF NUTRITION ON GROWTH AND DEVELOPMENT

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(With Plates 6–16 and Nine Text-figures)

CONTENTS

GENERAL INTRODUCTION TO PARTS II AND III.—METHODS AND MATERIALS

THE nature and implications of our approach to the problem of controlling the form and composition of the animal body have already been outlined, and the general lines of the experimental enquiries described.[1]

We have aimed at taking advantage of the fact that the different parts and tissues of the pig grow at different rates and are therefore

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[1] This is a continuation of work published in the previous number of the *Journal*: it is hoped to publish further parts in subsequent numbers of the *Journal*. A list of references will be given at the end of the concluding part.

likely to be differentially affected by differences in the rate of growth of the whole. From studies on the influence of varying degrees of under-nutrition upon the growth processes of the larger animals, there is a certain amount of experimental evidence in support of the latter possibility. Thus the pioneer work of Waters (1910), who placed cattle on a ration permitting no increase in weight, showed that while fat reserves were depleted, growth in skeleton as measured by length and height of the animal was not entirely inhibited. Similarly, Moulton *et al.* (1922) obtained differential effects upon the bone, and upon the lean and fat cuts of meat from beef cattle reared under different planes of nutrition. In sheep, Chirvinsky (1909) studied the effect of under-nutrition on the development of the skeleton and found that the thickness of bones was specially affected, those of the insufficiently nourished animals retaining the slender form characteristic of youth. In the pig, Henseler (1914) used extreme qualitative as well as quantitative differences in nutrition with a pair of animals and produced marked effects upon the body weight, form, and composition.

In respect to the major tissues, bone, muscle, and fat, these were such that bone was restricted least and fat most by the inadequate ration.

It is important to emphasize that our experiments differ from previous studies on the effect of varying planes of nutrition in that, rather than fixing the food intake at different levels and observing the results on growth, the animals have been made to grow along well-defined paths by controlling the food intake. The shape of the growth curve thus defines the plane of nutrition. The theoretical curves upon which the experiments are based (Text-fig. 1 of Part I) have already been described.

We have also been concerned, in this first series, solely with differences in the quantitative plane of nutrition. It is recognized that qualitative differences can produce marked effects upon growth, but it is logical to endeavour first to understand the consequences of the former before proceeding to a study of the latter. In any case, in so far as vital nutritive elements (vitamins, minerals, and certain amino-acids) are concerned, it seems probable that by far the most common qualitative differences in rations express themselves mainly through their effect upon the growth curve and to some degree at least will be covered by our quantitative study. Indeed, rate of growth is the most frequently accepted measure of many such differences.

With some animals severely restricted in the amount of food received, and others growing at as rapid a rate as they could be forced to attain

by ample supplies of the same ration, the danger of any qualitative deficiencies in the rations employed was guarded against in designing these. Thus it was considered essential to employ a ration rich in protein of high biological value, in minerals, and in vitamins. Partly for these reasons, separated milk was made the basis of the rationing scheme, while concentrates specially rich in proteins of animal origin were employed. There was an additional reason for both these points. We are especially interested in muscular development, and while the quantitative-qualitative association between protein nutrition and muscle growth has not been satisfactorily explained, the circumstantial evidence, together with a certain amount of experimental data supporting such a correlation (see Callow, 1935), made it desirable to give full opportunity for its expression should it exist. Highly rich protein rations are in any case the normal in many countries engaged in livestock production, and the writer's association with one of these has stressed the necessity for investigating the effects of such rations upon the animal body. The composition of the concentrate rations employed was as follows: '

	Mixture no. 1 (3–16 weeks)	Mixture no. 2 (16 weeks–200 lb.)
Dried separated milk (N.Z.)	20 parts	Nil
White fish meal	30 ,,	30 parts
Middlings	30 ,,	10 ,,
Flaked maize	20 ,,	30 ,,
Barley meal	Nil	30 ,,
Total	100 parts	100 parts

To this was added 4 oz. of cod-liver oil per 100 lb. of the mixture.

The general rationing scheme is set out below:

Ration while on sow:

    High Plane. Ad lib. separated milk and free access to mixture no. 1 in creep.

    Low Plane. Restricted access to sow and to mixture no. 1 and separated milk in creep.

Ration from weaning to 16 weeks:

    High Plane. 1 gal. separated milk daily per pig. Ad lib. mixture no. 1.

    Low Plane. ½ gal. separated milk daily per pig. Restricted amount varying with individual growth of mixture no. 1.

Ration from 16 weeks onwards:

    High-High. 1 gal. separated milk per pig daily. Ad lib. mixture no. 2.

High-Low.   ½ gal. separated milk per pig daily. Individual re-
          striction mixture no. 2.

Low-High.   1 gal. separated milk per pig daily. Ad lib. mixture
          no. 2.

Low-Low.   ½ gal. separated milk per pig daily. Individual re-
          striction mixture no. 2.

The commencement of restriction of the Low-Plane pigs occurred a
few days after birth, and was secured by removal of the Low-Plane
individuals from the sow for a variable and increasing number of hours
daily throughout the suckling period. Thus an 8 hr. period initially was
extended until at the normal weaning time at 56 days the Low-Plane
animals were virtually weaned. The actual time varied according to the
individual response. From weaning onwards the Cambridge individual
feeding technique for pig experiments (Dunlop, 1933) was followed as
far as was practicable. This was essential, and extremely useful with the
Low-Plane individuals and enabled more effective control over the shape
of the growth curve than was possible with collective feeding. Individual
feeding was practised from weaning, with the Low-High pigs until
16 weeks, and the Low-Low pigs until slaughter, and from 16 weeks to
slaughter with the High-Low pigs. Individual feeding was not found
practicable with the High-Plane animals. Maximum consumption was
considered essential for maximum growth rate, and this could not be
secured where, for technical and labour reasons associated with the
individual feeding system, the number of feeds per day had to be
restricted. High-Plane animals were thus fed in groups, but the number
of pigs in the latter was small and adjusted from time to time when
necessary to avoid the effects of competition. This limits the value of
our data from the food efficiency angle, but this was not our objective,
and group feeding by virtue of the design of the experiments is no
disadvantage to the critical study of those aspects which are our chief
concern.

All the pigs used were of the inbred strain and breeding can be seen
by reference to Appendix I (Part I). Within the limits of sex, the pigs
were randomized at birth to the respective treatments. The small number
of animals available resulted in the usual difficulty in avoiding sex
unbalance, and it will be noted that this occurs in one case in the bacon
series (Part III), while the proportion of males to females is in favour
of the latter within, though balanced between, the 16-week series
(Part II). Owing to the inbred nature of the material the necessity for

securing litter uniformity between treatments was not made an essential factor, though as far as possible litter-mates were allocated evenly to the various treatments. Half of the 16-week series were born in the winter of 1936–7 and the remainder in the following summer. The bacon pig series were all from the 1936–7 winter litters. Within these farrowings all pigs were born within a fortnight of each other and the majority within a week. The data obtained is described in two parts; in Part II, where the effects of a High and a Low Plane of nutrition from birth to 16 weeks upon body proportions and composition are described; and in Part III, where the effect of the four main treatments upon the 200 lb. bacon pig are compared.

The 16-week series consists of six pairs of High- and Low-Plane pigs—two of males (castrates) and four of females—and the 200 lb. series comprises five sets of the four treatments—three of males (castrates) and two of females.

PART II. EFFECT OF HIGH AND LOW PLANES OF NUTRITION BETWEEN BIRTH AND 16 WEEKS

(1) Live-weight growth curves

All animals were weighed at birth and thereafter weekly throughout the period, and from the resulting figures the mean live-weight growth curves of the High- and Low-Plane pairs (Text-fig. 19) and the curves of the individual pairs (Text-fig. 20) have been constructed. A greater mean live weight for the High-Plane animals at 16 weeks than that aimed at was obtained ($+13$ lb.) and a lower weight successfully achieved for the Low-Plane pigs (-13 lb.).

The weights at weaning (8 weeks old), however, were not as high as were desired for the High-Plane pigs, though the relative difference compared with the Low-Plane (20 lb.) was attained. The former averaged 40·7 lb.—a satisfactory result since the average weaning weight of pigs in this country is about 28 lb. (Davidson & Duckham, 1929–30).

Considerable difficulty was experienced in the early stages in slowing up the growth of the Low-Plane pigs, maintaining at the same time that of the High-Plane animals at a high level. This can be observed from both Text-fig. 19 and Text-fig. 20. From 3 to 5 days were allowed, depending upon the vigour of the individual concerned and the temper of the sow, before commencing the removal of the Low-Plane pigs for increasing intervals. Initially this had little effect upon weight. It appeared that for a time little, if any, deprivation of milk occurred. The

glands being suckled by the removed individuals were untouched by those remaining with the sow, and they apparently stored their supply which became available to the owners on their return. Donald (1937) has presented experimental evidence supporting this general preference of piglings for initially selected teats. After a fortnight, however, by which time the interval away had increased to 12–16 hr., it was noticeable that the glands suckled by the Low-Plane pigs had become smaller and
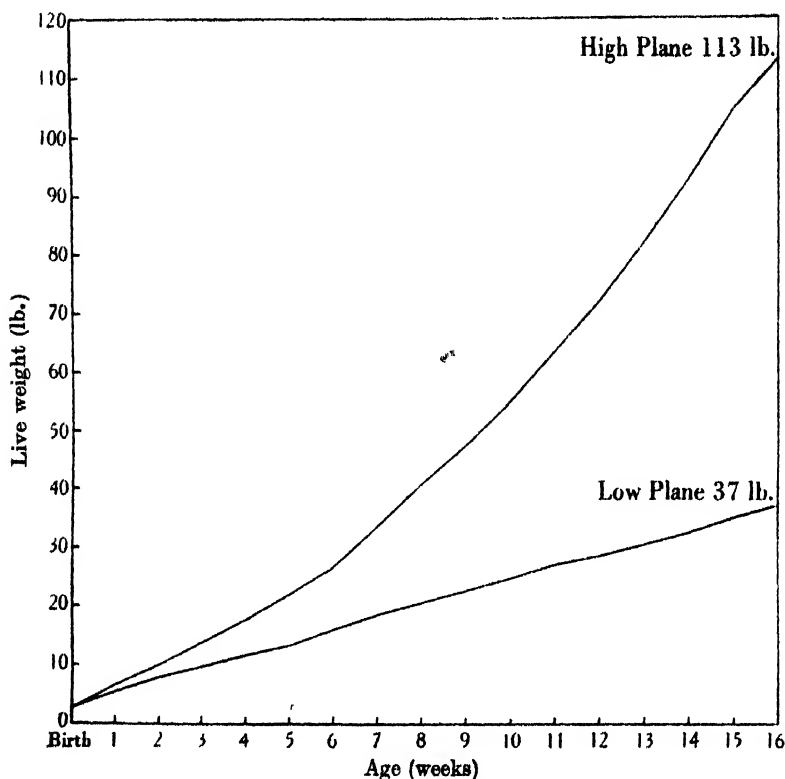
Text-fig. 19. Live-weight growth curves of High- and Low-Plane pigs from birth to 16 weeks. (Mean of six pairs.)

presented the appearance and feel of a diminishing milk yield. This situation progressively increased until at weaning these glands appeared quite dry. The general picture obtained is in line with our present knowledge of the physiology of milk production in the dairy cow (Hammond, 1936a), and the known effect of intermittent milking on yield. Well before any marked effect on weight was noticeable, the result of the treatment was clearly apparent in the appearance of the Low-Plane pigs whose skin became dry and scaly, with coarse hair, and whose growth appeared mainly one of bone.

During this period the growth of the High-Plane individuals was not aided by the removal of half the litter but, we believe, rather tended to be reduced by the necessity for frequent disturbance of the mother and litter during removal operations. Better control of the rate of growth of these was obtained after the 3-week stage when they began to take supplementary feed; from this stage onwards the difference in the curves became accentuated. The relative difference was still more marked after
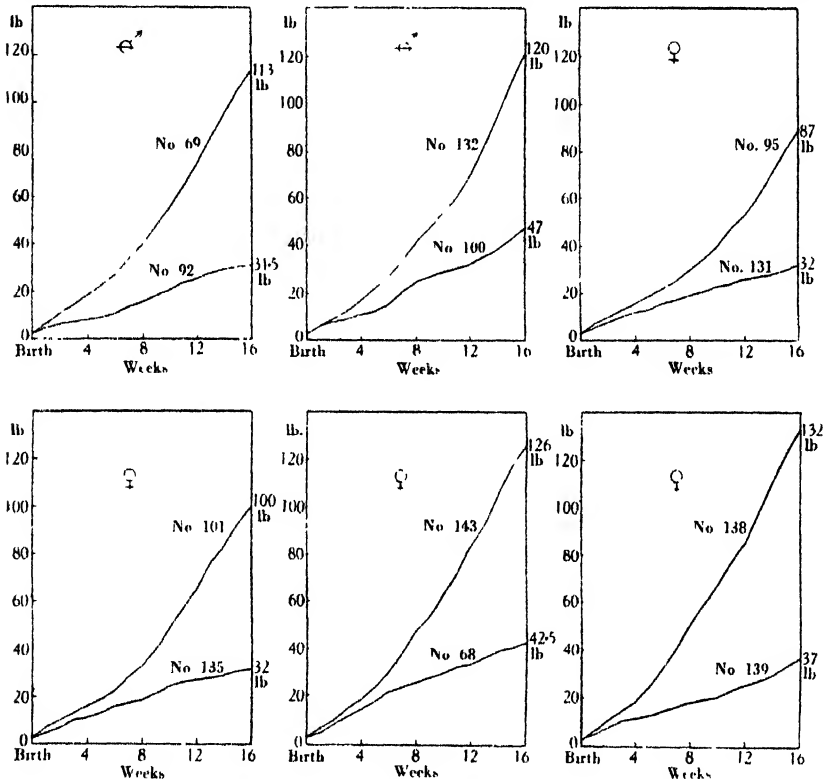
Text-fig. 20. Live-weight growth curves of High- and Low-Plane pigs from birth to 16 weeks.

weaning, when more controlled limitation of the ration of the Low-Plane individuals was possible (Pl. 6).

The variation in the individual curves is in part due to the factors we have mentioned. In addition, some of the Low-Plane pigs were remarkably vigorous (no. 100) and were extremely difficult to check, or had to be treated less severely owing to risk of loss (no. 68). Of the High-Plane pigs, no. 95, a winter-born animal, weaned at a low weight, and her subsequent growth rate is undoubtedly related to this. It may be a coincidence that the gland suckled by this animal was at the rear

end of the sow which is known to be associated with a lower milk yield (Olfsson & Larsen, 1930; Bonsma & Oosthuizen, 1935; Donald, 1937). It is of interest to record that the 3-week check in growth attributed to the normal decline in milk yield of the sow at this time, and the 8-week check at weaning commonly characteristic of pigs in this country (Kitchin, 1937) is not apparent in these pigs. Such checks could not be expected with the Low-Plane animals, and in the case of the High have probably been obviated in the first case by the use of milk in the creep, and in the second by the fact that the continued use of milk after 8 weeks meant that there was virtually no weaning.

Apart from the inherent difficulty of accurately measuring live weights, which (in addition to the factors already mentioned) undoubtedly exerted a considerable influence, the variability in the shape of the individual growth curves of these and also of the animals of Part III on the same plane treatment need not necessarily be attributed to genetic factors. Donald (1937) has shown that the variations in the weight of young pigs can be satisfactorily explained by differences in the level of nutrition consequent upon birth weight, suckling position in the teat line, and the variable milk yield of different sections of the mammary gland of the mother. These initial and uncontrollable variations are largely responsible for weight-for-age differences after the weaning stage (Wild, 1927; Thompson, 1931; Wenck, 1931; Murray, 1934; Schmidt & Zimmermann, 1934; Kitchin, 1937), which were only partly eliminated by subsequent control of the level of nutrition.

All the foregoing observations apply not only to the six pairs of animals under immediate consideration but to all pigs in both experiments up to the 16-week stage.

(2) Effect on body proportions

The relative effects upon body proportions have been studied photographically and by comparing the gross weights of the different parts (joints) of the body.

In Pl. 7 the pigs are shown all to the same shoulder-trotter height. This almost eliminates the difference in size (over three times in live weight—see Pl. 6) but in so doing provides a better picture of the relative effect on proportions. The plate has been prepared by printing to the same shoulder-trotter height the negatives obtained immediately after slaughter, cutting these out and pasting on squared paper, and rephotographing.

In the Low-Plane animals the foreparts of the body are relatively better developed than the hind. In the High-Plane pigs the reverse is the case. The heads of the former are large, and the face and neck relatively long. In the latter the heads are proportionately small, and face and neck short. Note also the proportionately larger ears in the former than in the latter. In the Low Plane, the legs are relatively long, and the body short and shallow. The hindquarters are poorly developed. In the High Plane, the legs are relatively short, and the body long and deep. The hindquarters are rounded and well developed.

It is clear that in the under-nourished animals the early-developing parts—head, ears, neck and legs—have been penalized relatively less by inadequate nutrition than the later-developing parts—the body depth, loin and hindquarters. In contrast to this, the High Plane of nutrition has favoured most the late-developing parts. The Low-Plane pigs have to a very large extent retained the proportions of the juvenile (see Age Series, Pl. 1, fig. 1, Part I), while the High-Plane animals approach the conformation of the adult. What variation there is within each lot is in line with the difference in body weight. Thus the heaviest Low-Plane individual (no. 100) is the best developed in the hindparts of the body, while the lightest High-Plane pig (no. 95) shows the least effect so far as the encouragement of late-developing parts is concerned.

The view shown in Pl. 7 provides the closest approach we have been able to obtain to the live form; photographs of the live animal are unsatisfactory owing to the impossibility of registering each pig in the same position. In Pl. 8 are shown the body proportions obtained by photographing the dressed carcass, and scaling all animals to the same body length, as measured from the tip of the hindtrotters and the tip of the snout.

These illustrate even more clearly the relative effect upon early- and late-developing parts; on the fore as compared with the hind end of the body. Note the relatively greater length of head, of neck, and of legs in the Low Plane as compared with the High. In the High Plane the hams are well rounded, the legs relatively short, and the loin much broader. Greater relative breadth is characteristic of the latter throughout the body.

These visual differences in body form are supported by the relative effect of the treatments upon the weight of the different anatomical joints of the body (Table 21). In this and in all succeeding tables of this series we have compared the relative effect of the plane of nutrition by expressing the weight of the part concerned in the High-Plane pigs as

Table 21. *Effect of plane of nutrition upon body proportions at 16 weeks*

	Mean weight (g.)		% carcass weight		Proportion Low Plane = 100	
Joint	Low Plane	High Plane	Low Plane	High Plane	Low Plane	High Plane
Head	1539	3217	14·56	8·99	100	209
Neck	877	3235	8·30	9·04	100	368
Shoulders (2)	2111	6252	19·95	17·49	100	257
Thorax	2221	9074	20·99	25·37	100	409
Loin	816	3675	7·70	10·27	100	450
Legs (2)	2240	7203	21·17	20·14	100	305
Pelvis	775	3111	7·33	8·70	100	402
Carcass weight	10579	35767	100·00	100·00	100	338

a percentage of the weight of the corresponding part in the Low-Plane pigs. This provides an effective measure not only of the relative effect as between treatments but also as between the different parts of the body of animals on the same treatment. The weight of the High-Plane part is given as a proportion of the weight of the Low-Plane part, with the latter as 100 in each case. The data is based in all cases on the "mean weights" calculated from the mean of the males and the mean of the females in each treatment. Mean weights and these as a percentage of the whole are also given. Raw data for the series are shown in Appendix III.

The weight of the head has been affected least and of the loin most by the treatment (see Text-fig. 21), the proportionate figures being 209 and 450. In the trunk joints the thorax and pelvis have been affected
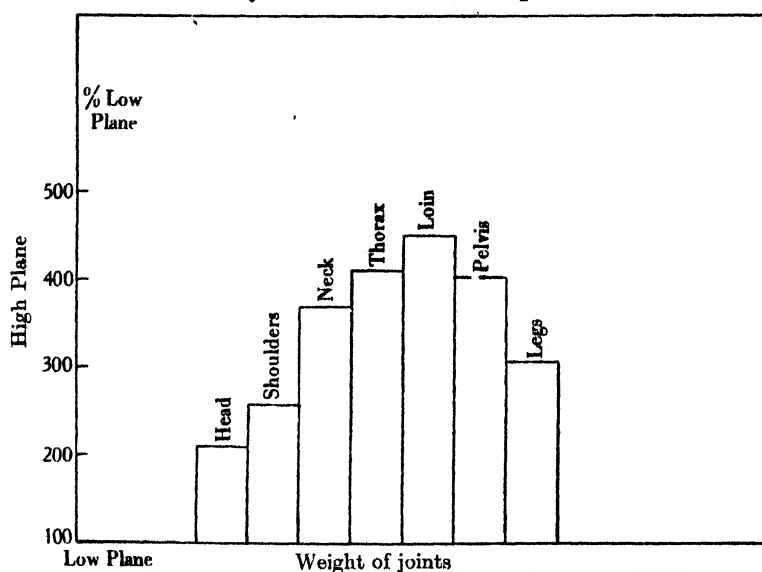
Text-fig. 21. Plane of nutrition, body proportions at 16 weeks.

to a similar and smaller degree than the loin, with the effect upon neck intermediate between that on the head and thorax. Note that the relative effect is in direct relation to the order of development as shown by our age series (see Table 1, Part I). This is supported by the effect on the limbs, these, as earlier-developing parts, being less affected than thorax, loin or pelvis, with the forelimb showing a smaller effect than the hindlimb.

These differences in relative effect can also be observed in the weights of each part as a percentage of the carcass weight. Thus the head accounts for 14·6 % of the carcass in the Low-Plane pigs as compared with 9 % in the High-Plane. Corresponding figures for the loin are 7·7 and 10·3 % respectively. These alone, however, are not satisfactory as a measure of relative effect, since they are affected by the proportion that one part plays to another.

It is clear that the Low-Plane animals are not miniatures of the High-Plane, but that the plane of nutrition has produced a marked differential effect on the body.

(3) Effect on body composition (bone, muscle, fat, skin and organs)

Analysis of the dissection data reveals even more strongly marked differential effects upon the component body tissues (Table 22).

The dressed carcass weight of the High-Plane pigs is 3·38 times as great as that of the Low-Plane. This is higher than the relative difference in live weight due to the smaller proportional effect (2·72 times) on the body organs and offals (Table 25). The composition of the respective carcasses is markedly different. The Low-Plane pigs have a higher

Table 22. *Effect of plane of nutrition on composition of carcass at 16 weeks*

Plane of nutrition	Mean weight (g.)		% carcass weight		Proportion Low Plane = 100	
	Low Plane	High Plane	Low Plane	High Plane	Low Plane	High Plane
Skeleton	2032	4550	19·20	12·71	100	224
Muscle	5622	16366	53·14	45·76	100	291
Fat	1092	10993	10·32	30·73	100	1007
Skin	867	1835	8·20	5·13	100	212
Tendon, glands, waste, etc.	643	1287	6·08	3·60	100	200
Loss in dissection	323	736	3·06	2·07	—	—
Carcass weight	10579	35767	100·00	100·00	100	338
Muscle/bone	2·77	3·60	—	—	100	130
Fat/bone	0·54	2·42	—	—	100	450

percentage of bone, muscle, skin, and tendon and glands, but a lower percentage of fat. This situation clearly reveals the inadequacy of live or carcass weight as measures of the effect of nutritional treatments.
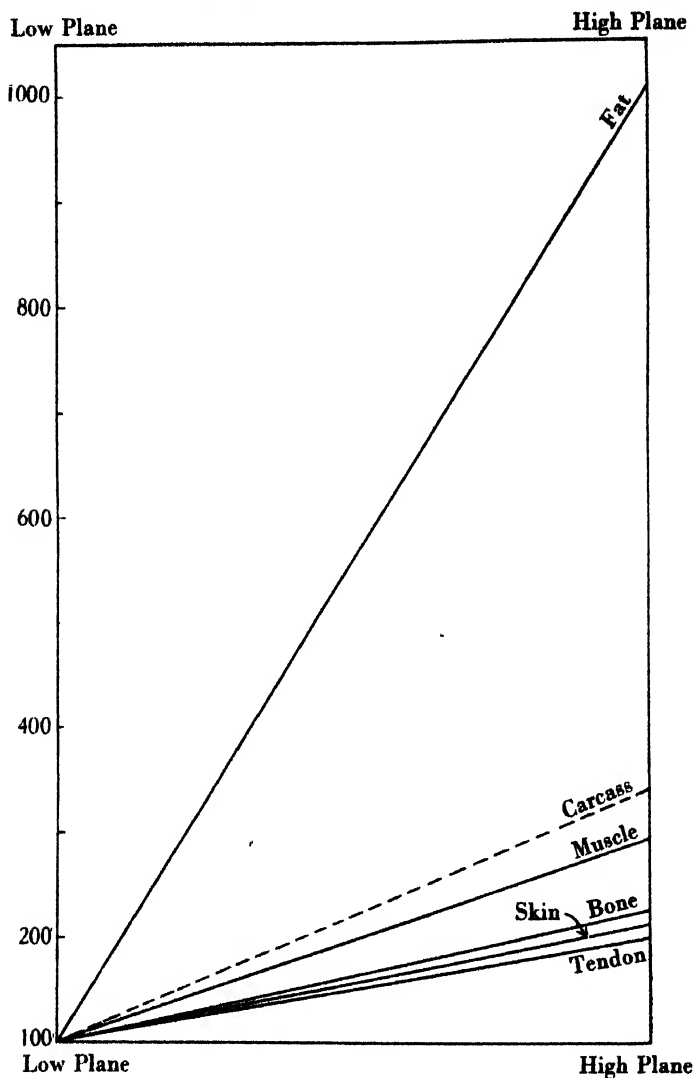
Text-fig. 22. Plane of nutrition, carcass composition at 16 weeks.

The relative effect on the different tissues is shown in diagram form in Text-fig. 22.

Of the three major tissues, bone has been affected least, muscle next, and fat most, the proportionate figures being 221, 291, and 1007. The effect on skin and tendon is comparable with that on the skeleton, being only slightly less.

Growth in skeleton—the earliest developing of the major tissues—has persisted to a remarkable degree in the under-nourished animals; growth of fat, however, has been almost entirely inhibited. In the High-Plane pigs, the growth of bone and muscle has been stimulated but not to the extent that characterizes fat. The relative effect upon these tissues is of great importance from a meat quality viewpoint. The ratio of muscle
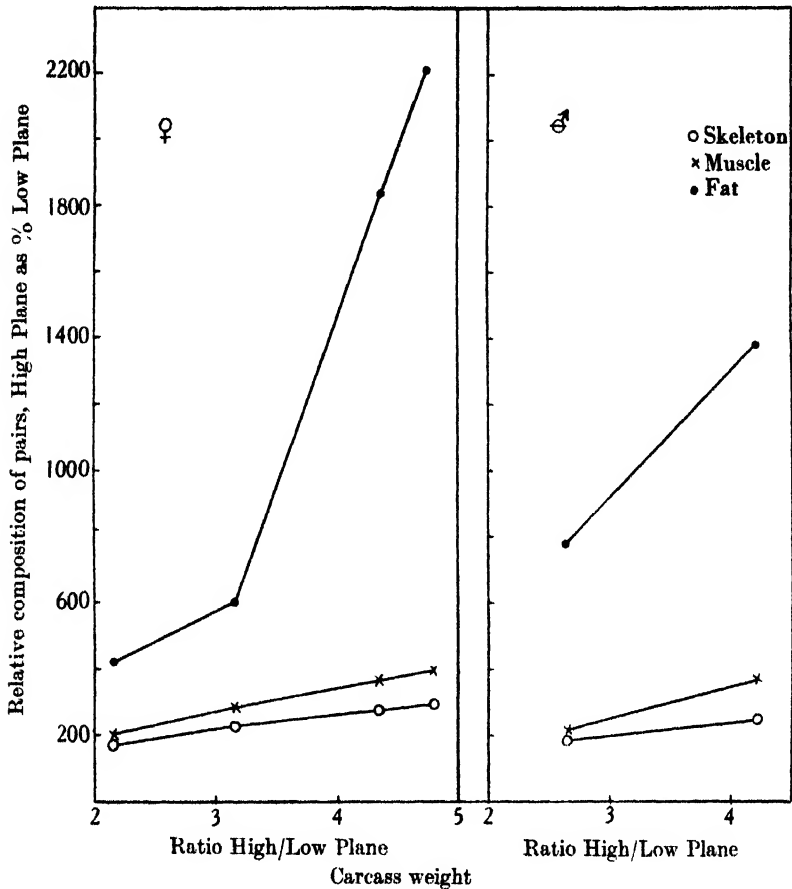
Text-fig. 23. Effect of increasing difference in the plane of nutrition at 16 weeks.

to bone is much higher in the High-Plane animals despite the lower percentage muscle under this treatment. A high muscle/bone ratio is an essential characteristic in the good meat animal. Relative difference in the fat/bone ratio is even greater, amounting to a 450 % higher figure.

The close similarity between the picture so far presented and that obtained from our examination of the growth of these tissues with age is very striking (compare Text-fig. 5, Part I with Text-fig. 22); those that

show the smaller relative effect are those which develop earlier in life, and the relative order of effect of the plane of nutrition is the same as the order of development of the different parts. It would appear that not only does nutrition affect the body differentially, but that it does so in an orderly manner.

Table 23. *Effect of increasing difference in plane of nutrition on body composition at* 16 *weeks*

(Individual pairs arranged in order of carcass-weight difference)

Sex	Pair numbers H.P.	Pair numbers L.P.	Carcass weight Ratio $\frac{H.P.}{L.P.}$	Skeleton	Muscle	Fat	Organs
Hogs	69	100	2·66	185	217	781	213
	132	92	4·21	249	370	1382	342
		Mean	3·3	214	278	1018	262
Gilts	95	68	2·16	170	202	420	234
	101	139	3·16	225	282	604	241
	143	135	4·35	275	367	1843	329
	138	131	4·79	295	395	2218	341
		Mean	3·47	236	305	995	283

(The columns "Skeleton", "Muscle", "Fat", "Organs" fall under the heading: Relative composition of High-Plane pigs, Low-Plane pigs = 100)

In Text-fig. 23 we have plotted the relative effect of the plane of nutrition on the bone, muscle, and fat, against the ratio of carcass weight of the High- and Low-Plane *individuals* with the latter arranged in order of carcass-weight difference. The sexes are shown separately and the relevant data given in Table 23. They provide strong supporting evidence for the mean results. In both sexes, the relative effect increases in the case of each tissue, as the weight difference between the High- and Low-Plane pairs increases. The curves for muscle fall on a higher level than those for bone, with an increasing difference between them as the High/Low carcass-weight ratio increases. The effect on fat, similarly, is much greater at the higher weight differences than at the lower, and in all cases is relatively higher than the effect on the other tissues.

(4) Effect on organs

The mean weights and the relative effect of the plane of nutrition on the main groups of body organs and offals are compared in Table 24 and of the individual organs in Table 25. The relative effect is also shown in diagram form in Text-fig. 24.

In respect to the major groups, while we find that the relative effect is on a lower level than that of later-developing tissues already compared, quite large differential effects exist between the different units. Thus the

earliest-developing group, the skin, hair and hoofs of the well-nourished animals, is but 188 % of the poorly fed. The thoracic organs are 238 % and the abdominal group (exclusive of alimentary tract) 368 % of the Low Plane. These and the effects on the other units are, in the main, in line with the order of development. One notable exception occurs as between the thoracic group and the alimentary tract. In our age series we found the tract to be the later-developing part; here, however, it is less affected than the thoracic group. This situation is due to the relative effect of nutrition upon the individual components of these groups, and possible reasons for this will be advanced when discussing the latter.

Table 24. *Effect of plane of nutrition on development of organs* at 16 years*

	Mean weight of part (g.)		Percentage empty live weight		Proportion Low Plane = 100	
	Low Plane	High Plane	Low Plane	High Plane	Low Plane	High Plane
Empty live weight	14640	47014	100	100	100	321
Skin, hair, hoofs	287	540	1·96	1·15	100	188
Blood	944	2788	6·45	5·93	100	295
Total glands	89·5	241	0·61	0·51	100	269
Thoracic organs	417	994	2·85	2·11	100	238
Abdominal organs:						
Alimentary tract	1132	2366	7·73	5·03	100	209
Remainder	866	3190	5·92	6·79	100	368
Total abdominal†	1998	5556	13·65	11·82	100	278
Total organs*	3736	10119	25·52	21·52	100	271

* Including parts removed as offals, and excluding genital organs.
† Excluding genital organs.

Note that each group has also been expressed as a percentage of the "empty live weight". All subsequent comparisons with live weight have been made on this basis as a means of avoiding the variable "fill" of the animals. Empty live weight is the live weight immediately prior to slaughter less blood and the contents of the alimentary tract and bladder. Total organs and offals amount to a higher proportion of the empty live weight in the Low-Plane pigs.

Of the individual organs, it will be noted that, except for a few outstanding cases, the relative difference between the two planes is on a low level and round about 200 %. Examination of the outstanding divergencies reveals the interesting situation that while some of the parts showing the relatively largest effects are those which we know to be late-developing, there are some that have been influenced to a considerable extent by the difference in nutrition, though under normal conditions of growth they have shown themselves to be relatively early-developing.

Table 25. *Effect of plane of nutrition on development
of individual organs at 16 weeks**

	Mean weight of part (g.)		Percentage empty live weight		Proportion	
	Low Plane	High Plane	Low Plane	High Plane	Low Plane	High Plane
Empty live weight	14640	47014	100	100	100	321
Hair and skin	271	497	1·85	1·06	100	183
Hoofs: Fore	9	24	0·06	0·05	100	267
Hind	7	18·5	0·05	0·04	100	264
Blood	944	2788	6·45	5·93	100	295
Neck thymus	14	100	0·10	0·21	100	714
Heart thymus	7·5	33	0·05	0·07	100	440
Lymphatic and salivary glands†	68	108	0·46	0·23	100	159
Diaphragm	76	224	0·52	0·47	100	295
Heart	73	180	0·50	0·38	100	246
Pericardium and blood vessels	44	125	0·30	0·27	100	284
Lungs and trachea	224	465	1·53	0·99	100	208
Oesophagus	21	35	0·14	0·07	100	167
Stomach	187	332	1·28	0·71	100	178
Small intestine	576	1265	3·93	3·11	100	220
Caecum	43	90	0·29	0·19	100	209
Large intestine and rectum	307	645	3·00	1·37	100	210
Caul	5·5	46	0·04	0·10	100	836
Mesentery	124	518	0·85	1·10	100	418
Liver	558	1624	3·81	3·45	100	291
Gall bladder	5·4	30·5	0·04	0·07	100	564
Spleen	23	52	0·16	0·11	100	226
Pancreas	32·5	105	0·22	0·22	100	323
Kidneys	69	283	0·47	0·60	100	410
Kidney and leaf fat	34·5	508	0·24	1·08	100	1472
Bladder	13·5	25·5	0·09	0·05	100	189
Uterus and vagina	18	124	0·12	0·26	100	689
Penis and vesicula seminalis	28·5	59·5	0·19	0·13	100	208
Total organs	3757	10210	25·66	21·72	100	272

* Including parts of body removed as offals.
† Excluding lymphatics of alimentary canal.

Thus, of the former, the functionally late-developing, fat-containing parts—the mesentery, caul, kidney and leaf fat—show relative differences of 418, 836 and 1472 % respectively as between the High- and Low-Plane pigs. Internal fat, as well as body fat, has been restricted in the underfed animals and encouraged in the well-fed. Similarly, the functionally late-developing sex organs of the females have been relatively much influenced with a difference of 689 % in favour of the High-Plane animals. This is in marked contrast to the relative difference in the sex organs of the castrates of only 208 % which is understandable in view of the removal of the testicles. The former result is in agreement with that of McKenzie

(1926), who found that a low plane of nutrition retarded the development of the female genital organs of pigs.

Parts showing a relatively greater effect than could be expected, if the differential influence of nutrition follows only the order of development, are the blood at 295 %, the liver at 291 %, pancreas at 323 %, kidneys at 410 % and the thymus gland at 618 %.
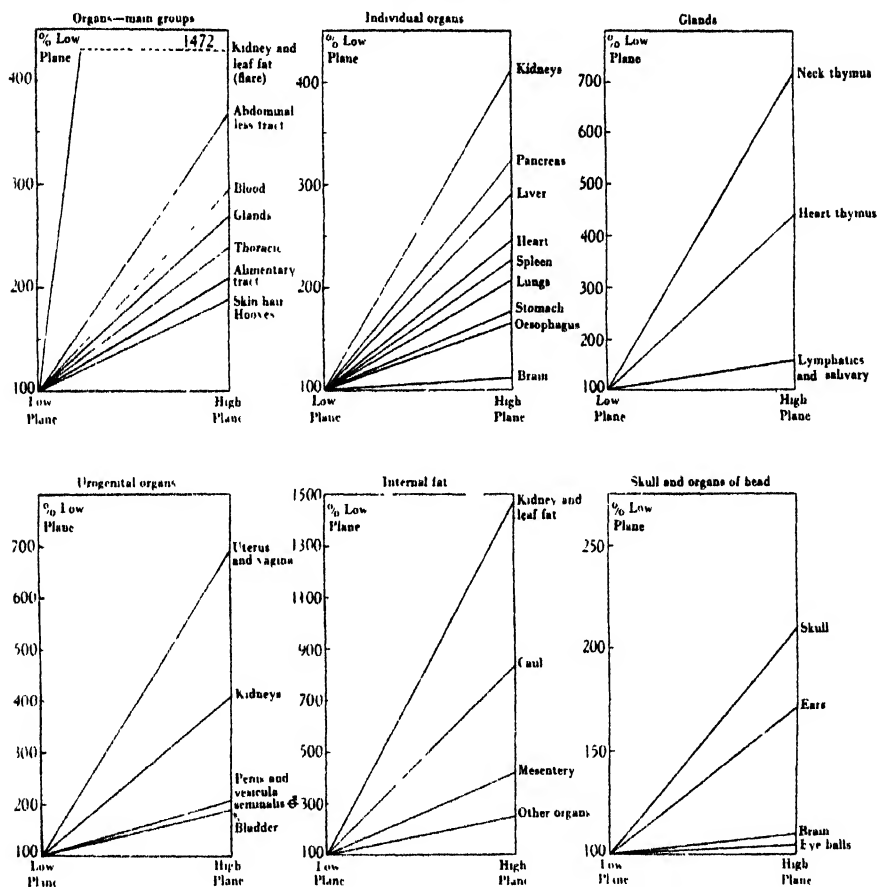
Text-fig. 24. Relative effect plane of nutrition on development of organs at 16 weeks.

In respect to the blood it is possible that the result is due on the one hand to the higher level of metabolism of the High-Plane pigs and on the other to the general low level that must have characterized the Low-Plane animals, leading to a greater production of blood in the former case. It is of interest that the relative difference in blood is of the same order as that in total muscle; in our age series too, blood and muscle followed a similar growth curve, though the latter showed a

somewhat greater relative development. Similarly, the effect on the pancreas might be explained on metabolic grounds, the functional demands on this organ being likely to be greater under conditions of high than low food intakes.

In the liver and kidneys, a further factor—that of the level of protein nutrition—is likely to be involved. The use of an abnormally rich protein diet—about six times the usual proportion of protein concentrates was employed—must have necessitated a considerable amount of extra work in deamination for both these organs. This would be likely to be far greater in the case of the High-Plane pigs where the protein surplus over normal requirements for growth was unusually high. Pugliese (1904) demonstrated that the weight of the liver and its content of total nitrogen increased during feeding and reduced during fasting. Luck (1936) showed that in rats on a high-protein diet, as compared with a low, certain protein fractions increased their amount by over ten times, and that the increased weight of the livers of the high-plane animals was due, not only to hypertrophy, but also to an increased protein content per unit of tissue. In the kidney, Woodman *et al.* (1936), using a lower level of protein nutrition than we have employed, obtained significantly higher kidney weights in pigs on high-protein diets and attributed this to a functional adaptation consequent on the necessity for deamination of the surplus protein.

Photographs of the kidneys of each pig are shown in Pl. 9 (all to same scale). Those of the High-Plane animals were perfectly normal in shape and appearance, and retention cysts commonly believed to be associated with high-protein diets were entirely absent except in one kidney of pig 95. This was small and its site can be observed in the photograph. The kidneys of the Low-Plane animals were also normal except for pig 92, where the abnormality is developmental and not in any way attributable to the high protein or to under-nutrition. The condition is commonly met with in pigs and is believed to be due to incomplete differentiation in embryonic life (see pathologist's report, Part III). Such kidneys are believed to function perfectly normally, and the occurrence of a similar case in our next series of pigs provides interesting confirmation of this. We have as yet no evidence as to whether the tremendous difference in size is associated with hyperplasia or hypertrophy, or with both; work on the histology side is in progress.

The relative effects of the two treatments upon the thymus gland are of very great interest, particularly in relation to its behaviour after the 16-week stage (Part III). It is generally recognized that this gland is

precocious in its growth behaviour, and many workers are interested in its relation to growth processes. Whatever the precise position in this respect it is very clear that the weight of the thymus is by no means a function of age, but that it is very much influenced by the rate of growth or plane of nutrition of the animal. Our results here are in accord with those of McCarrison (1921), who found that starvation made for losses in the thymus at any age. Any association with growth would thus appear to be indirect rather than direct.

Mention was made earlier of the relative difference in the behaviour of the thoracic organs and the alimentary tract, and the unexpected inverse order of the effect on these parts. It will be seen that the larger difference between the High- and Low-Plane animals is the result of the relatively large effect upon the heart, pericardium and blood vessels, and the diaphragm. In view of the similar large effect upon the blood, that on the associated organs is not remarkable, while the better development of the diaphragm in the High-Plane animals is probably associated with the considerable fat deposition in and about this muscle, as well as with the general stimulation of all muscles under good nutrition.

The relatively small difference in the weights of the alimentary tract under the two treatments is also apparent in the lengths of the small intestine, caecum, large intestine, and rectum, where the relative difference is of the order of 130 % in favour of the High-Plane pigs (Table 26).

Table 26. *Effect of plane of nutrition on length of alimentary tract at 16 weeks*

	Mean length (cm.)		Percentage total length		Proportion Low Plane = 100	
Part	Low Plane	High Plane	Low Plane	High Plane	Low Plane	High Plane
Small intestine	1475	1955	83·7	82·9	100	132
Caecum	15	20·5	0·85	0·87	100	137
Large intestine and rectum	274	377	15·5	16·0	100	138
Total	1764	2352	100	100	100	133

The effects on the organs of the head are compared in Table 27 and relative to other organs in Text-fig. 24. Despite a 338 % difference in body weight, the weight of the eyeballs and the weight of the brain is practically the same in both sets of pigs. The mean figures give the High-Plane animals only a 4 % superiority in eyeballs and 11 % in brain. The former difference is not statistically significant. The earliest-developing of the body organs are thus neither encouraged by good nor

retarded by poor nutrition in their growth The results are of interest in relation to the recent work of Donaldson *et al.* (1937) on the eyes of the rat, from which it was concluded that the eye was unique in its growth and that its weight was largely a function of age In comparing their results with those of Jackson (1913) and Moment (1933) they suggest that the divergencies from this situation are possibly due to differences in nutrition From our results, however, it is clear that even very extreme differences in the quantitative plane of nutrition fail to influence the eyeballs of pigs It might also be noted that these are the organs found to be resistant to the effects of thyroidectomy by Hammett (1929).

Table 27. *Effect of plane of nutrition on development of skull and organs of head at 16 weeks*

Part	Mean weight (g.)		Proportion Low Plane = 100	
	Low Plane	High Plane	Low Plane	High Plane
Eyes	9·0	9·4	100	104
Brain	82	91	100	111
Ears	132	228	100	173
Skull	313	654	100	209

While presenting on first examination some appearance of anomalous behaviour, it will be recognized that the relative effects of different levels of nutrition upon the body organs and offals are in line with our general thesis; as a whole, and as in normal growth, they have apparently first call on available nutrients, and under conditions of under-nutrition are less retarded in their growth than less essential and later-developing parts. Marked differential effects are noticeable, however, and these are such that a functional basis offers a reasonable explanation of the differences in response just as it did in providing an explanation for their differential growth with age.

(5) Effect upon the skeleton

The relative effect of the plane of nutrition upon the total skeleton at 16 weeks has been shown to be less than on the other tissues; as with the latter, differential effects are distinguishable in respect to its various parts, though in keeping with the small effect upon the whole, these are smaller in degree than is the case with muscle and fat in different parts of the body (see Text-fig. 25). Though this is the case it is significant that the proportional differences in the effect of nutrition upon the skeletal units follow a trend closely related to that of the effects upon muscle and fat of comparable anatomical regions (Text-fig. 25).

Actual and relative differences in the main bone groups under the two treatments are shown in Table 28. The effect of the difference in nutrition increases from head to tail, with the head bones the least affected and the pelvis the most affected. Of the vertebral column, the relative difference in weight is greatest in the lumbar region and least

Table 28. *Effect of plane of nutrition on development of skeleton at 16 weeks*

Part of body	Mean weights (g.)		Percentage total skeleton		Proportion	
	Low Plane	High Plane	Low Plane	High Plane	Low Plane	High Plane
Head:						
Skull	313	654	15·4	14·4	100	209
Lower jaw	109	217	5·36	4·8	100	200
Tongue bones	4	7	0·20	0·15	100	175
Vertebral column:						
Cervical	96	201	4·72	4·42	100	209
Thoracic	194	419	9·55	9·21	100	216
Lumbar	108	252	5·31	5·54	100	233
Sacral	34	77	1·67	1·69	100	226
Ribs and sternum	244	580	12·00	12·75	100	238
Pelvis	102	250	5·02	5·50	100	245
Forelimb (2)	407	948	20·02	20·81	100	233
Hindlimb (2)	416	934	20·47	20·53	100	225
Total skeleton	2027	4539	100	100	100	224
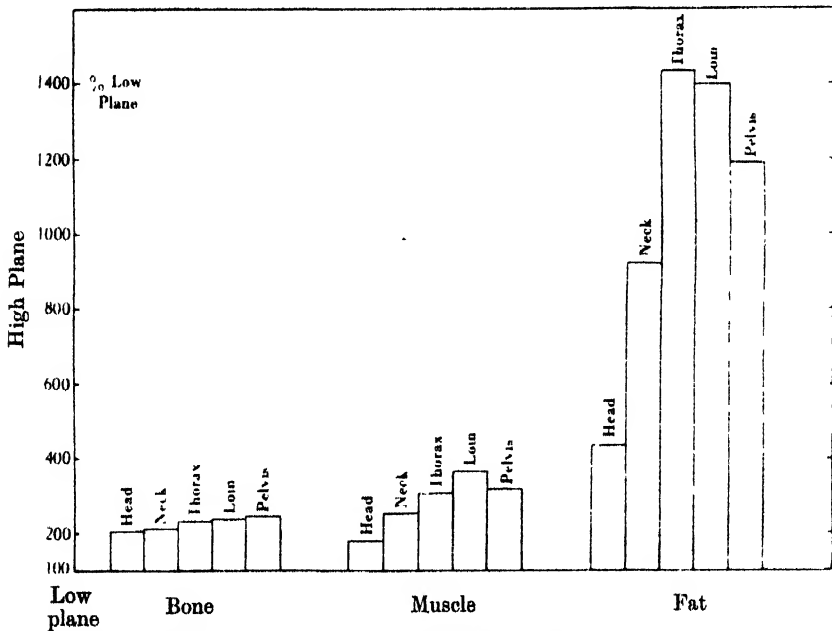
Text-fig. 25. Plane of nutrition—proportion of bone, muscle, and fat in different parts of body at 16 weeks.

in the cervical. The leg bones of the hindlimbs are influenced to the same extent as the skeleton as a whole, but those of the forelimbs slightly more. The effect on the ribs and sternum is relatively large.

Table 29. *Effect of plane of nutrition on development of limb bones at 16 weeks*

	Mean weights (g.)		Percentage total limb bones		Proportion	
	Low Plane	High Plane	Low Plane	High Plane	Low Plane	High Plane
Forelimbs (2):						
Scapula	70	198	17·1	20·8	100	283
Humerus	142	317	34·8	33·4	100	223
Radius ulna	100	218	24·5	23·0	100	218
Carpals	23	54	5·7	5·7	100	235
Splints	9	20	2·2	2·1	100	222
Cannons	31	65	7·6	6·9	100	210
Total leg	374	872	91·9	91·9	100	233
Pasterns	12·3	28·4	3·0	3·0	100	231
Coronets	7·2	16·8	1·7	1·7	100	233
Dew claws	5·9	15·8	1·7	1·6	100	229
Naviculars and sesamoids	2·1	6·8	0·5	0·7	100	323
Pedals	4·9	10·6	1·2	1·1	100	216
Total foot	33·3	78·4	8·1	8·1	100	235
Hindlimbs (2):						
Femur	156	345	37·5	36·8	100	221
Patella	9	21	2·2	2·2	100	233
Tibia-fibula	113	255	27·1	27·3	100	226
Astragalus	25	51	6·0	5·5	100	204
Calcaneum	24	55	5·8	5·9	100	229
Tarsals	16	41	3·8	4·4	100	256
Splints	7	16	1·7	1·7	100	228
Cannons	34	76	8·2	8·1	100	224
Total leg	384	860	92·3	91·9	100	223
Pasterns	12·5	29·7	3·0	3·1	100	238
Coronets	7	17·7	1·6	1·8	100	253
Dew claws	5·4	13·2	1·3	1·4	100	240
Naviculars and sesamoids	2·2	5·8	0·5	0·6	100	264
Pedals	4·8	10·8	1·2	1·2	100	225
Total foot	31·9	77·2	7·6	8·1	100	241

The influence upon the individual bones of the limbs is shown in Table 29. The outstanding feature here is the fairly regular effect and the absence of any well-defined gradient up the limb. It will be remembered (see Part I) that it was only in the later stages of growth that the upper limb bones began to show any marked difference in growth rate. Up to 5 months—where the weight of the animals is comparable with these—little difference was apparent. This might be the reason for

the present situation—for the cannon bones showing just as large a relative difference between the two planes of nutrition as the femurs. Though over a longer age period the former may make relatively less total growth than the latter, in the early stages both grow at rapid and similar rates. With the effect of nutrition on bone relatively slight in any case, the absence of a differential effect at 16 weeks is not, therefore, incompatible with the general effect being greater on the later-developing parts. It will be noted that there is some suggestion of a greater relative influence upon the upper bones of the limb as compared with the distal in the case of the scapula and the pelvis which are much affected. The relative effect upon the astragalus and calcaneum, too, might be mentioned. During the early stages of life the former is always the heavier bone, but it is overtaken later by the latter which thereafter continues to increase its advantage. It is significant that in the Low-Plane animals this relative position has been hindered, with the result that the astragalus is still the heavier bone. In the High Plane, the position is reversed and the relative weights are characteristic of much older ages.

Differences in the size and form of some of the major bones and bone groups are illustrated in Pls. 10–15. These have been selected so as to provide a picture of the effects upon different parts of the trunk and limbs.

The relative effects of good and poor nutrition upon the development of the skull are of special importance to the breeder of stock who has long been accustomed to use the form of the head as an index of quality in his animals. The size and shape of the skull will obviously be a controlling factor here. The relatively longer and narrower faces of the Low-Plane animals has already been commented upon. That these are due to similar differences in the shape of the skulls is clearly evident from Pl. 10. The differences in absolute size are striking when it is remembered that the skull is one of the least affected bones and that bone is one of the least affected tissues. Relatively, however, the difference is less in total length than in width. Length growth has been penalized less than thickness growth by under-nourishment, while in the well-fed animals the latter has been encouraged relatively more. This can be seen in the relative widths of the zygomatic arches which are at least twice the thickness in the High- as compared with the Low-Plane pigs. The latter have approximately four-fifths the total skull length of the former. The difference is also shown up in the relative thickness through the craniums which averaged 18 mm. in the High Plane and only 3 mm. in the Low

Plane. The cranial cavity was similar in size in both treatments, as might be expected from the similarity in brain weights.

While at first sight the form of the head might appear to have little connexion with the fattening capabilities of the animal, these differential responses obtained to different levels of metabolism, as induced by control of the external level of nutrition, offer a clue to the reason for so using it by the animal breeder. He is perhaps inclined to attribute differences in the proportions of the head solely to inherent differences in metabolic efficiency. The dangers of such an assumption will be clear from this demonstration of the capacity of nutrition to produce considerable modification in these proportions. The situation also raises the question of the reliability of methods of classifying breeds into classes on a basis of the shape of the head by Sanson (1910), Diffloth (1922) and Dechambre (1922), a point which will receive further emphasis when the form of the skulls of the bacon pigs are compared.

Differences in the form of the ribs are shown in Pl. 11. Special attention is drawn to these because of the relationship of the depth of the chest and the heaviness of the fore-end of bacon-pig carcasses to quality (Hammond & Murray, 1937). A high body length/weight ratio is an essential character in a bacon pig, and this necessitates a relatively narrow and light fore-end. The proportion of waste in the fore-end is also related to the weight and form of the bones of this area. The illustration, which is of the sixth rib only, shows considerable difference in both length and thickness in favour of the High-Plane animals; as with the skull the relative differences is greater in thickness than in length.

A similar difference is apparent between the lumbar vertebrae of the two sets of pigs (Pl. 12). Length has been restricted less than thickness growth in the Low-Plane animals. This situation can also be verified by inference from the relative effects upon length and weight. The proportionate figures are of the order of 125 % for the former and 233 % for the latter.

Pl. 13 shows the influence of nutrition upon the pelvis which is greater than on any other major bone group and amounts to 245 % in weight. Differences in size and shape are also considerable and of interest in view of the incidence of contracted pelvis in humans and the greater association of such defects with conditions of poverty and congestion (McLennan, 1937). In this connexion the subsequent behaviour of the pelvis of the Low-Plane animals under a change in the level of nutrition and under a continuation of a general low level may afford experimental

evidence of the reality or otherwise of such an association. It is probable, however, that the contracted pelvis of humans is due more to qualitative than quantitative nutritional deficiencies, for it is most frequently associated with infantile rickets (Harris, 1937). If, as is our aim, our rations have provided against qualitative deficiencies we should not find pelvic abnormalities. At this stage no obvious abnormality in the shape of the pelvis under the two treatments is noticeable; those of the Low-Plane animals are typical of the juvenile form. The relative difference in length and width—between the acetabulum joints, and between the wings of the ilium—is slightly greater than comparable differences in the bones already studied. As with the latter, however, the effect has been greater upon the thickness growth than on length.

The femurs as typical bones of the upper part of the limb, and the cannons of the lower part are shown in Pls. 14 and 15. The relative differences are similar to those we have noted in respect to the other bones. Note the relatively greater size of the epiphyses of the High-Plane animals particularly in the case of the femurs. More precise evidence upon the relative development of length and thickness growth is afforded in Table 30, where the maximum length of the bones is

Table 30. *Effect of plane of nutrition on length and thickness (weight/length) growth in bone at 16 weeks*

Pig no.		Length (mm.)			Weight (g.) / Length (mm.)		
L.P.	H.P.	L.P.	H.P.	$\frac{H.P.}{L.P.} \times 100$	L.P.	H.P.	$\frac{H.P.}{L.P.} \times 100$
			Femur				
92	69	117·7	156·7	133	0·618	1·059	171
100	132	126·0	156·8	124	0·710	1·177	166
68	143	132·2	160·1	121	0·666	1·156	174
131	95	120·6	146·4	121	0·572	0·970	170
135	101	120·0	154·3	128	0·596	1·063	178
139	138	123·5	159·1	129	0·587	1·169	199
	Mean	122·3	155·7	127	0·625	1·099	176
			Hind cannons				
92	69	51·9	71·7	138	0·298	0·516	173
100	132	56·0	73·0	130	0·357	0·562	157
68	143	59·8	76·4	128	0·309	0·550	178
131	95	55·6	68·3	123	0·270	0·469	174
135	101	54·0	67·5	125	0·278	0·496	178
139	138	56·2	75·0	133	0·284	0·513	181
	Mean	55·6	72·0	129	0·299	0·518	173

compared with the weight/length ratio. In the femur, the relative effect is of the order of 127 % for length and 176 % for the weight/length ratio.

The figures for the individual pairs of animals are in fair agreement, what variability exists being explainable on a basis of the relative weight differences of the pigs. The data for the cannon bones are of similar order.

Summing up the position it can be said that in form even more than in weight the plane of nutrition is capable of exerting differential effects upon the different bones of the skeleton. These effects are such that the later-developing bones and the later-developing characteristics (thickness growth as compared with length) are influenced to a proportionately greater extent.

(6) Effect upon muscle in different parts of the body

More clearly than bone, the relative effect upon muscle of the plane of nutrition exhibits a well-defined gradient from the early-developing to the late-developing parts of the body. Thus the muscles of the head are affected least and the loin most with neck and thorax intermediate in that order (Table 31 and Text-fig. 25). The pelvis muscles are affected slightly less than those of the loin. Here also, the limb muscles as a whole behave as early-developing parts with the hindlimb indicating its later-developing character by exhibiting a slightly greater effect.

Table 31. *Effect of plane of nutrition on development of muscle at 16 weeks*

Part of body	Mean weights (g.)		Percentage total muscle		Proportion	
	Low Plane	High Plane	Low Plane	High Plane	Low Plane	High Plane
Head	376	674	6·69	4·11	100	179
Neck	533	1352	9·48	8·26	100	254
Shoulders:						
Shoulder	1091	2877	19·40	17·57	100	264
Arm	125	328	2·22	2·00	100	262
Cannon	7·3	18	0·13	0·11	100	247
Total	1223	3223	21·75	19·68	100	264
Thorax	1277	3912	22·71	23·90	100	306
Loin:						
Psoas	111	393	1·97	2·40	100	354
Loin	389	1405	6·91	8·58	100	361
Total	500	1798	8·88	10·98	100	360
Legs:						
Leg	1090	3452	19·39	21·00	100	317
Arm	216	671	3·84	4·10	100	310
Cannon	10	29	0·18	0·18	100	290
Total	1316	4152	23·41	25·28	100	316
Pelvis	400	1258	7·11	7·69	100	314
Total muscle	5622	16366	100	100	100	291

Within the limb muscles the various units in both fore- and hindlimbs show a gradient in the effect between the lower and upper parts. In each case the muscles round the cannon bones are least affected, and those of the shoulder and thigh, in fore- and hindlimbs respectively, show the greatest effect. Muscles of the arm and leg are intermediate between these. Relative effect, then, follows their order of development.

In respect to the loin muscles, note that the psoas behaves as a relatively late-developing part and shows a large effect. The psoas, because it is removed in commerce and is thus readily available, has
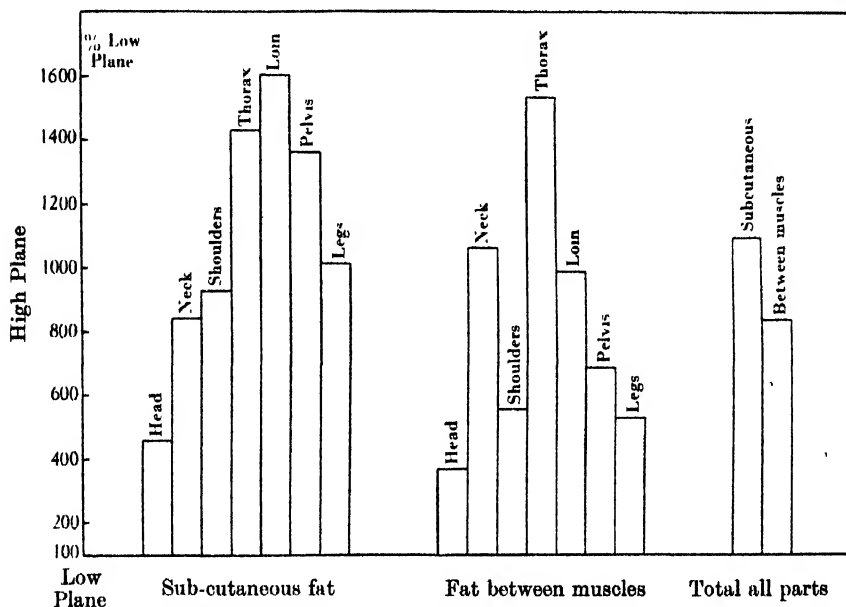
Text-fig. 26. Relative effect of plane of nutrition on fat in different parts of body at 16 weeks.

been used by Callow (1935a) and Woodman et al. (1936) as a sample muscle in endeavouring to measure the effect of nutritional treatments on muscular growth. If it can be agreed that the selection of a later-developing part rather than an early is likely to provide a more efficient index of the state of the development of the musculature as a whole—and this can be argued on the grounds that such a muscle is more likely to show up differences if such exist—the use of the psoas for this purpose would appear to have some justification. These relative differences in the effect on muscle in different parts are of considerable significance from a meat production point of view; the provision of a high plane of nutrition has tended to encourage relatively most those muscles situated in the most valuable parts of the meat animal—the hind- rather than the

forequarters. On the other hand, inadequate nutrition appears to have restricted most the musculature of these areas.

(7) EFFECT UPON FAT IN DIFFERENT PARTS OF THE BODY

The relative effect upon subcutaneous, intermuscular and total fat in the different regions is shown in Table 32.

Table 32. *Effect of plane of nutrition on development of fat at 16 weeks*

Part of body	Mean weights (g.)		Percentage total fat		Proportion	
	Low Plane	High Plane	Low Plane	High Plane	Low Plane	High Plane
Head:						
Subcutaneous	91	418	8·33	3·80	100	460
Intermuscular	62	242	5·68	2·20	100	390
Total	153	660	14·01	6·00	100	431
Neck:						
Subcutaneous	94	791	8·61	7·19	100	841
Intermuscular	55	585	5·04	5·32	100	1063
Total	149	1376	13·65	12·51	100	923
Shoulders (2):						
Subcutaneous	110	1022	10·07	9·29	100	929
Intermuscular	84	468	7·69	4·25	100	557
Total	194	1490	17·76	13·54	100	768
Thorax:						
Subcutaneous	158	2264	14·47	20·59	100	1433
Intermuscular	80	1227	7·33	11·16	100	1538
Total	238	3491	21·80	31·75	100	1472
Loin:						
Subcutaneous	69	1107	6·32	10·07	100	1604
Intermuscular	26	223	2·38	2·03	100	988
Total	95	1330	8·70	12·10	100	1400
Pelvis:						
Subcutaneous	76	1038	6·96	9·44	100	1365
Intermuscular	26	178	2·38	1·62	100	685
Total	102	1216	9·34	11·06	100	1192
Legs (2):						
Subcutaneous	117	1189	10·71	10·81	100	1017
Intermuscular	47	247	4·30	2·25	100	527
Total	164	1436	15·01	13·06	100	876
Total subcutaneous	714	7826	65·38	71·20	100	1096
Total intermuscular	378	3167	34·62	28·80	100	838
Total fat	1092	10993	100·00	100·00	100	1007

In every joint the effect upon fat has been far greater than upon bone or muscle. Within the trunk joints a marked differential effect

comparable with that in respect to the other tissues is apparent (Text-fig. 25). The gradient in total fat, however, is such that the thorax depots show the maximum effect, while in the case of muscle the loin occupied this position. From Text-fig. 26 it is clear that this situation is due to differences in the relative response of subcutaneous and intermuscular fats.

The position provides extremely good support for the suggestions advanced in respect to these two types of fat in our examination of their behaviour with age (see Part I). We argued that intermuscular fat as classified by us consisted of two types, one of which, more correctly described as "permanent deposit fat", is similar in function and growth behaviour to the subcutaneous. It will be seen that with subcutaneous fat alone the gradient from head (least affected) to loin (most affected) is well marked. Pelvis fat is less affected than the loin, while the limbs occupy their expected positions as early-developing regions. With inter-muscular fat the position at first sight appears less orderly; the relative influence upon the thorax and neck outstrips all others. These two areas, however, are those where the largest amounts of fat of the "permanent deposit" character exist between the muscles, and in the case of the High-Plane pigs the extent of these was considerable and characteristic of an advanced stage of fattening. If the true intermuscular fat be in reality earlier-developing than subcutaneous and the latter type the position becomes understandable, and in line with the general argument that the plane of nutrition will affect the late-developing parts most. The loin is another joint where a large amount of storage fat is deposited between the surface muscles with fattening, and it will be noted that in this area, too, the relative effect of nutrition upon the intramuscular fat is high.

The picture is also supported by the relative influence upon total subcutaneous and total intermuscular where the amount of the per-manent deposit type of intermuscular fat is sufficient to reduce the relative difference but insufficient to eliminate it.

(8) Effect upon carcass measurements

The relative differences between the carcass measurements of the High- and Low-Plane animals are in close agreement with those we have observed between the bodies as a whole, their proportions, and their composition (Tables 33, 34). The general picture so presented gives promise of useful correlations between measurements and composition.

Of the *external* measurements, length of leg, length of body, length of carcass, and depth of chest have been affected in that order, while in the forearm the length of trotter has been influenced least, the length of the forearm next, and the circumference of the forearm most by the difference in treatment. The relative effects are illustrated in histogram form in Text-fig. 27, which also permits a comparison with the effects upon other measures. It will be noted that the relative effects upon linear body measures, which are largely measures of differences in
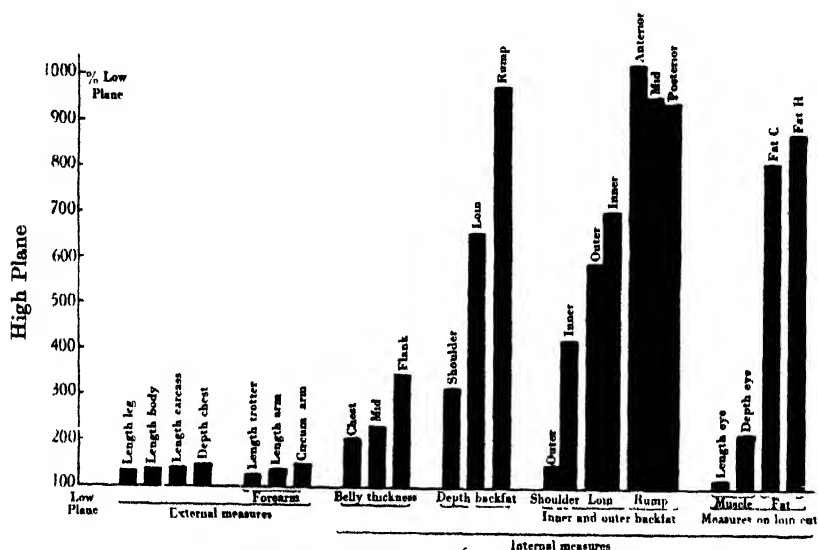
Text-fig. 27. Relative effect of plane of nutrition on carcass measurements at 16 weeks.

skeletal development, are much less than on "internal" measures which are more directly related to the composition of the animal. In respect to the former, too, the order of effect bears, as in the latter also, a direct relation to the order of development.

The proportional effect on the belly thickness is on a relatively high level consistent with its muscle and fat content, and a gradient in effect is noticeable in an anterior-posterior direction.

Relative effect is greatest in respect to the fat measurements; of these the maximum effect is upon the rump measures and the least upon the shoulder thickness, with loin-fat thickness showing more than double the effect on the latter. The difference in the relative position of the loin and pelvis as shown by measurements and weights of fat respectively is no doubt due to the relatively small amount of fat affected by the rump measures. The fat measurements have been compared in more detail in

Table 33. *Effect of plane of nutrition on body and carcass measurements at 16 weeks*

	Length of			Depth Chest	Length Trotter	Forearm		Back-fat thickness		
	Leg	Body	Carcass			Length	Circum- ference	Shoulder	Loin	Rump
				Mean measurements (mm.)						
Low Plane	649	463	185	372	67	135	131	10·1	1·9	2·0
High Plane	894	647	274	495	86	183	195	31·7	12·4	19·4
				Proportional effect						
Low Plane	100	100	100	100	100	100	100	100	100	100
High Plane	138	140	148	133	128	136	149	314	653	970

	Belly thickness			Cut at last rib					
	Chest	Middle	Inguinal	Eye A	Eye B	Shape index	Fat C	Fat H	Skin
			Mean measurements (mm.)						
Low Plane	10·9	10·0	6·7	58	15	260	1·6	2·3	2·5
High Plane	22·2	23·0	23·2	69	32·8	475	12·9	20·0	2·4
			Proportional effect						
Low Plane	100	100	100	100	100	100	100	100	100
High Plane	204	230	346	119	218	183	806	870	96

Table 34. *Effect of plane of nutrition on back fat measurements at 16 weeks*

		Mean measurements		Proportion	
		Low Plane	High Plane	Low Plane	High Plane
Shoulder fat:	Outer layer	3·9	5·8	100	149
	Inner layer	6·2	25·9	100	418
Loin fat:	Outer layer	0·8	4·7	100	588
	Inner layer	1·1	7·7	100	700
Rump fat:	(1) Anterior	2·3	23·3	100	1013
	(2) Median	1·5	14·2	100	947
	(3) Posterior	2·2	20·5	100	932
	Mean back fat	4·6	21·1	100	460

Table 34, where the relative influence of high and low nutrition on the inner and outer layers is clearly apparent. The outer layer, the earliest-developing part of the back fat, is affected to a much smaller degree than the inner layer, within which the great bulk of deposit fat is laid. This relative difference is greater at the shoulder than at the loin, a result in line with the relative growth with age of the two layers, at the fore- as compared with the hind-end of the body (see Part 1, Table 13). In the Low-Plane pigs, the outer layer has been relatively more restricted by under-nutrition in the later-developing loin region than in the earlier-developing shoulder region. On the other hand, in the High Plane, the outer layer has been relatively speeded up more in its development in

the later-developing loin by good feeding. The net result is a marked reduction in the shoulder/loin outer layer ratio in the High-Plane pigs.

The relative effect upon the measurements on the *loin cut* show a smaller effect upon muscle than on fat and a larger effect upon the "depth of the eye" (measure *B*, Text-fig. 1, Part I) than upon the "length of the eye" (measure *A*). We have previously drawn attention to the suggested relationship between bone thickness and muscle thickness (Part I) and to the later-developing character of both as compared with length growth. Pl. 16 provides a comparison of the relative composition of the pigs as revealed by the cross-section at the last rib, and upon which these measures have been taken. Here, to show differences in proportions (bone, muscle and fat), rather than in size, the sections have been scaled to the same eye muscle length (measure *A*, Text-fig. 1, Part I).

Note the greater relative depth of eye muscle in the High-Plane animals, and the relatively greater proportion of bone in the Low-Plane. The plate also clearly shows up the relative proportions of muscle and fat, as well as the differences in the body form of the two sets of animals. Differences within each set are in line with the differences in body weight. These are given in the plate to facilitate comparisons.

(9) EFFECT ON HISTOLOGY AND COLOUR OF MUSCLE

Since no significant differences were found between the fibre diameters of the three muscles examined in the age series, histological work in the present series has been confined to one, the longissimus dorsi, sampled at the junction of the loin and thorax. For this, measurements of the fibre diameter have been recorded on fifty fibres per animal, while sections prepared by the freezing method and stained with Sudan III were examined for differences in intramuscular fat (marbling fat).

Table 35. *Influence of plane of nutrition on size of muscle fibre*
(longissimus dorsi) at 16 weeks

(Mean diameters—50 fibres per pig. 1/6 and 4 eyepiece)

	Low Plane		High Plane
Pig no.	*M*	Pig no.	*M*
92	8.32 ± 0.323	69	12.12 ± 0.415
100	8.56 ± 0.344	132	12.58 ± 0.414
68	8.08 ± 0.345	143	11.30 ± 0.318
131	8.66 ± 0.313	95	10.26 ± 0.404
135	8.74 ± 0.384	101	12.22 ± 0.314
139	8.78 ± 0.379	138	14.00 ± 0.409
Mean	8.523 ± 0.122	Mean	12.08 ± 0.561

Table 35 *a*. *Effect of plane of nutrition on colour of muscle
at* 16 *weeks*

(Comparison of individual pairs of pigs)

		Low Plane			High Plane	
	Pig no.	Diaphragm	Longissimus dorsi	Pig no.	Diaphragm	Longissimus dorsi
air 1	92 ♂	10 B	5 P	69 ♂	5 P	3 P
„ 2	100 ♂	10 B	5 P	132 ♂	10 B	5 P
„ 3	68 ♀	9 B	4 P	95 ♀	10 B	2 P
„ 4	131 ♀	10 B	5 P	101 ♀	5 P	4 P
„ 5	135 ♀	9 B	5 P	138 ♀	6 P	3 P
„ 6	139 ♀	5 P	5 P	143 ♀	4 P	4 P

B = Beef scale (dark: 10 darkest); P = Pork scale (pale: 2 palest).

Mean diameters of the muscle fibres of each pig together with the respective standard errors are given in Table 35. The treatment mean in each case has been calculated direct from the mean fibre diameter of each individual. The plane of nutrition has clearly exerted a significant effect upon fibre size, each High-Plane animal having considerably larger fibres than its Low-Plane mate. The mean fibre diameter of the High-Plane pigs is approximately 50 % larger than that of the Low Plane. The differences are illustrated in Part III. The variation in the fibre size of the High-Plane pigs is relatively high. It will be noted, however, that this variation is closely related to differences in the live weights and the weights of muscle of the different pigs. Thus the heaviest individual (no. 138) and the lightest (no. 95) have the largest and smallest muscle fibres respectively.

Waters (1909) obtained similar nutritional effects on the size of the muscle fibre of steers, showing that increase occurred under good nutrition and reduction on a subnormal diet. Hammond (1932a) reviews the literature in respect to other species which show a similar response. He also records the large differences in the muscle-fibre size of relatively unimproved and primitive breeds of sheep like the Shetland and Soay, kept under poor nutritive conditions, and highly improved breeds reared on high nutrition as the Suffolk. Rubli (1931) similarly draws attention to the smaller fibres of the wild boar as compared with the domesticated pigs. In view of our results this is likely due to the lower nutritive conditions of the wild pig.

In respect to the development of marbling fat under the two treatments, the pictures presented by the sections are illustrated in Part III. The Low-Plane pigs showed practically no such fat, that existing being present in the form of isolated fine streaks. The High-Plane, on the other

hand, showed a relatively large quantity, distributed in a network between the muscle bundles. These results are in agreement with the relative difference in the chemically extracted intramuscular fat of the thorax muscle (see § 10).

The effect of nutrition upon colour of muscle can be seen from Table 35 a, where the colour of the diaphragm and the longissimus dorsi have been measured by a standard colour scale. Since age, which we have shown to influence the colour of muscle in the pig, is the same for all animals, any differences will be due to nutrition and/or exercise. On the average, the High-Plane pigs have lighter coloured muscles for both diaphragm and longissimus dorsi. The former muscle, as in the age series, is darker than the latter, an effect which must be attributed to the greater activity of the diaphragm (Part I, § 9). The slightly darker colour of the Low-Plane animals in respect to both may be attributed to exercise also, the effect of nutrition being indirect in that the well-fed animals tended to live a more placid, less active existence than the Low-Plane which were restless and active in their demands for food.

(10) Effect upon chemical composition of muscle and fat

The chemical side of these investigations is in the hands of Dr E. H. Callow of the Low Temperature Research Station, Cambridge. Only a limited amount of data is as yet available.

The writer is, however, indebted to Dr Callow for pushing forward

Table 36. *Effect of plane of nutrition on chemical composition of muscle and subcutaneous fat at 16 weeks*

	Pig no.	Plane of nutrition	Muscle							
			Psoas				Thorax (longissimus dorsi)			
			Fat %	Tissue %	Water %	Iodine no.	Fat %	Tissue %	Water %	Iodine no.
Hogs	92	Low	0·98	18·24	80·78	99·1	0·83	19·89	79·28	87·7
	69	High	2·27	21·21	76·52	70·1	2·26	22·80	74·94	64·4
Gilts	135	Low	1·00	18·87	80·13	88·6	0·53	22·57	76·90	103·2
	138	High	3·23	21·47	75·30	64·4	2·28	23·89	73·83	61·5

	Pig no.	Plane of nutrition	Subcutaneous fat							
			Outer layer				Inner layer			
Hogs	92	Low	12·23*	16·34*	71·43*	61·3*	—	—	—	—
	69	High	86·99	3·52	9·49	66·7	86·05	3·86	10·09	60·5
Gilts	135	Low	11·87*	14·71*	73·44*	75·9*	—	—	—	—
	138	High	88·45	3·33	8·22	61·5	89·93	2·56	7·51	55·7

* Outer + inner layer.

preliminary analyses on two animals on each treatment, together with two on each treatment at 200 lb. (Part III), so as to enable some idea of the effects upon chemical composition to be gauged and related to our anatomical study.

From examination of the chemical results available from the age series (Part I) it was decided that samples from the region of the thoracic-lumbar junction would provide a reasonable picture of the chemical composition of muscle and fat tissue as a whole. In Table 36 are presented the results for two muscle samples, and for the inner and outer layers of subcutaneous fat from this region. Of the former, one is the psoas muscle which has the additional advantage that it is a complete muscle unit. The data cover one hog and one gilt pig in each case.

The plane of nutrition has exerted a marked influence upon the percentage fat, tissue, water, and iodine number of the fat of both muscle and fat tissues. In respect to the former, in both psoas and thorax muscle, the percentage fat and percentage tissue (residue) is lower, and the percentage water higher in the Low-Plane pigs. This follows for both the hogs and gilts. By comparison with the results of Table 18 (Part I), it will be observed that the Low-Plane pigs at 16 weeks have a composition similar to that of the pig at birth in respect to water and residue, with an even lower content of fat. The latter result, a difference of over 100%, is of interest in relation to our histological observations in respect to intramuscular fat. Under a low nutritive level from birth, the relatively high fat content on the muscle of the new-born pig has been considerably reduced. The free fat globules to which we attributed the latter condition, and which normally disappear with age, have not been proportionately replaced by marbling fat. The position is consistent with our suggestion that this initial fat has some immediate energy function, and with the relation of nutrition to fat deposition. As compared with this situation, the muscles of the High-Plane animals have a composition typical of much older pigs, the value being consistent with the 20–28-week animals of the age series.

The treatment has exerted a very large effect upon the chemical nature of the fat, the iodine numbers being much greater in the Low-Plane pigs in both muscles and in both hogs and gilts. The figures for the under-fed pigs are well beyond the range normally met with in pig work and are characteristic of animals fed large quantities of extremely unsaturated oils (Callow, 1935). The ration used, however, has been one that would tend to produce a saturated fat (Part III). The position is consistent with the growth-rate theory of iodine value (see Part I, § 10),

the fast-growing High-Plane animals having produced a relatively saturated, and the slow-growing Low-Plane pigs an unsaturated type of deposit fat. Note that the iodine value of the latter bears no relation to the relatively saturated intramuscular fat of the new-born pig. This supports the suggestion inherent in the foregoing that what little fat is present in the latter has been laid down during growth, and has been derived almost, if not entirely, from food oils. On the other hand, the relatively saturated nature of the fat of the High-Plane pigs points to synthesis from other than food oils as its major source. In respect to the effect of the treatments upon the composition of the subcutaneous fat, the position is unfortunately somewhat obscured by the necessity for bulking the inner and outer layers in the Low-Plane pigs. It was not found practicable to separate the two layers in consequence of the relative thickness (see § 9) and texture of each. The bulk sample will probably resemble more the outer than the inner layer which was but poorly developed.

Differences in relative fat content are extremely large, the High-Plane pigs having by far the greater percentage. In consequence, the water content is equally high in favour of the Low-Plane pigs which also have the larger percentage of tissue. The Low-Plane pigs tend to resemble the new-born (Table 17, Part I) also in their subcutaneous fat, having but little more fat and a similar water content; the High-Plane have a composition comparable with the 20-week pigs. In iodine values, the differences are not so well defined; in the hog pair the High-Plane pig has a more unsaturated outer layer than the bulk sample of the Low-Plane pig; in the gilt pair, the Low-Plane pig has the more unsaturated fat. The former result is not consistent with the growth theory in respect to this character, and the reason for this situation is not clear. Further results from the other pairs of animals are required before it will be justifiable to speculate as to the possible reasons. Differences between the inner and outer fat (High-Plane only) provide the same comparison as available in the age series; the inner layer is relatively more saturated than the outer, a result which is in line with their relative rates of deposition.

While the data available are too scanty to draw any definite conclusions they are in the main consistent, and the differences large. They point to definite and understandable influences of the plane of nutrition of the animal upon the chemical composition. These differences are such that the under-fed pigs resemble the juvenile and the well-fed the older animal; the former may be regarded as physiologically younger and the

latter physiologically older than is normal at this age. The parallelism between this situation and the relative effect upon anatomical composition needs no emphasis. It may be noted, however, that since the fat content of the tissues studied is much lower in the Low-Plane than in the High-Plane pigs, the relative effect of the treatment upon the "true fat content", as distinct from "fat tissue", will be even greater than that which we have recorded in respect to the latter.

(11) Discussion

The major impression which the foregoing analysis must leave is the profound influence of nutrition upon the animal body. The imposition of extreme differences in the quantitative plane of nutrition upon pigs over the same age period has produced outstanding differences in the development of the resulting individuals. These are such that, though identical in their chronological age, the animals may be considered to be widely different in their physiological age. A high plane of nutrition operative from birth has so accelerated the growth of the proportions, organs, and tissues that the animals have attained a more advanced stage of development than is normal for their age. A low plane, on the other hand, has slowed up growth to an extent which has produced individuals developmentally retarded. The effect has not been one of simple acceleration and of slowing down in the rate of growth; the under-nourished animals are not miniatures of the well fed, for the different parts of the body have reacted differentially in each case to the nutritive supplies available.

Equally outstanding has been the parallelism between the relative response to nutrition of the different parts of the animal body and the relative order in development of these parts. An inadequate nutritive supply restricts most the late-developing parts of the body; an ample supply encourages most these same parts. So close is this relationship that the arrangement of the various parts in order of increasing relative effect gives precisely the same picture of anterior-posterior gradients in the trunk and of centripetal gradients in each limb as were obtained from examination of age changes. In fact, the evidence available from the present study suggests the existence of a supplementary gradient from the region of the tail forward to the loin. This possibility was also apparent in data of the age series. We thus obtain a picture of growth gradients in the pig extending from the six extremities—head, four feet, and tail—toward a common meeting ground in the latest-developing lumbar region. More detailed mapping may reveal this as an over-

simplification of the position; any modifications which may need to be introduced, however, are unlikely to alter the position materially, and the picture as here presented provides an extremely illuminating basis for thé study and interpretation of growth changes in relation to carcass quality in the pig. It will also be noted that the results obtained suggest an interesting modification of the usual methods of studying growth changes in the animal. Rather than comparison of large numbers at different ages and/or weights the imposition of high and low levels of nutrition upon comparable individuals and the measurement of the relative response of the different parts can provide valuable information on growth.

This relationship between the nature of the nutritional response of different parts of the body and their relative order in development provides a clue to the underlying reason for the effects obtained. In consequence of their differential growth, the tissues of the animal compete differentially for available nutritive supplies. By virtue of their greater growth intensity, earlier-developing parts have a prior claim in available nutrients. If these be in short supply, growth in late-developing parts is penalized, while the greater competitive capacity of the earlier-developing parts enables these to continue their growth. Conversely, an ample supply of nutrients, by eliminating the severity of this competition, enables relatively more and earlier growth of an otherwise late-developing part. This conception of the nature of the effects of nutrition on the animal body has been employed by Hammond (1932a) in studying the differences between different breeds and types of sheep and pigs. The primitive breeds relative to breeds improved for meat purposes show greater differences in late- than in early-developing parts of the body. The improved breeds have been evolved from the primitive by selection under the stimulus of higher nutritive conditions which, reacting upon the body in the differential manner we have described, have resulted in a proportionately greater development of the late-developing parts in the former as compared with the latter. In some breeds the process has been carried further than in others, with the result that earlier-maturing breeds have a greater proportionate development of their late-developing parts than late-maturing breeds. In this study with closely inbred animals we have obtained a comparable result through the influence of nutrition alone. The Low-Plane pigs resemble not so much the juvenile as the primitive and unimproved form; the High-Plane not so much the adult as an earlier-maturing type in which the development of normally late-developing units has been advanced. The comparisons which will be

afforded by the experiment of Part III should provide interesting material from this point of view. Walton & Hammond (1938) have recently published the results of an ingenious experiment similarly illustrative of the differential nature of the growth response of the body to nutritional differences. By making reciprocal crosses between an extremely large (Shire) and an extremely small (Shetland) breed of horse they have shown that the restriction of nutrition *in utero* in the case of the foal from the small mother, as compared with the foal from the large mother, resulted not only in a smaller animal at birth but in animals between which the major differences lay in the late-developing parts. In the case of these foals the initial effects have persisted throughout life. In the next section we will be concerned with the problem of how far the differences produced upon the pigs of this series persist when the animals are grown to the same final live weight.

(12) Summary

No attempt will be made to give a detailed summary of all the findings of the present experiment. It is rather our purpose to draw attention to the main principles emerging.

1. The influence of extremes of high and low planes of nutrition during the first 16 weeks of post-natal life upon the growth in body proportions and in anatomical composition has been studied experimentally in six pairs of closely inbred pigs. Quantitative differences in nutrition operative from birth have resulted in an average live weight at 16 weeks of 113 lb. in the High-Plane and 37 lb. in the Low-Plane animals.

2. In body proportions, the head, ears, neck, legs, and body length are penalized relatively less by inadequate nutrition than are body depth, loin, and hindquarters. Conversely, good nutrition favours most the latter characters. These effects upon body form are similarly evident in the gross weight of the different anatomical regions involved. Low-Plane animals to a large extent retain the proportions of the juvenile and High-Plane approach the conformation of the adult.

3. These differential effects upon body form are the result of even more marked differential effects upon the body tissues. Thus of the major tissues, skeleton weight is affected relatively less than the weight of muscle and muscle relatively less than is total fat. In the High-Plane pigs the skeleton was 221 %, muscle 291 %, and fat 1007 % of the weight of these tissues in the Low-Plane animals. Effect upon skin, tendon, and glands was slightly less than on the skeleton.

4. The effect upon organs and offals is relatively less than upon either live or carcass weight. Thus the difference in the total organ weight was of the order of 200 % in favour of the High-Plane pigs as compared with 338 % in the dressed carcass weight. Within the organs, however, marked differential response to nutrition occurs. The differences recorded ranged from 104 % in the most resistant organs to 1472% in the least resistant. The nature of the response is such that a functional basis provides an explanation in the same way as it explained the differential growth of organs with age.

5. The differential effect of different levels of nutrition upon both proportions and tissues is closely related to the differential rates of growth of these characters, and to their relative order of development. Late-developing parts of the body, compared with early, are penalized proportionately more by under-nourishment and encouraged more by ample nutritive supplies. This result may be interpreted as a superiority in the competitive capacity of early-developing units of the body for available nutrition.

6. Just as between the major tissues, so within the anatomical units of each, marked differential effects are produced. In all three tissues — bone, muscle, and fat—the arrangement of the different regions of the body in order of increasing effect provides precisely the same picture of anterior-posterior growth gradients in the head and trunk, and of centripetal gradients in each limb, as is evident from examination of growth changes in the pig with age. This situation is apparent also in the order of effect in body proportions, early-developing parts being affected less than late.

7. The plane of nutrition not only affects the weight of the individual skeletal units in a differential and orderly manner, but it produces comparable effects upon the form of the bones. Thus the late-developing thickness growth is influenced to a proportionately greater extent than the earlier-developing length growth of bones.

8. The relatively large response of muscle to nutrition is closely related to the effect upon the size of the muscle fibre; this is markedly reduced by under-nutrition and well developed by good feeding.

9. The subcutaneous fat is affected to a greater extent than the intermuscular fat. This confirms the later-developing character of the former tissue. Regional differences in subcutaneous fat provide a particularly clear-cut picture of growth gradients of the type described.

10. The effects upon the body as measured by external and internal carcass measurements are in complete agreement with the behaviour of

the parts and tissues for which the respective measurements provide an index. Thus linear measures on the body surface, due to their relationship to the resistant skeleton, show a proportionately smaller response to nutrition than internal carcass measures of muscle and fat.

11. Differences in the chemical composition and nature of the muscle and fat tissues are similarly in line with the hypothesis that the differential response of body tissues to nutrition is due to their differential rates of growth and the consequent prior claim of earlier-developing parts to available nutritive supplies.

(To be continued)

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APPENDIX III

Total composition of carcass at 16 weeks (g.)

	Low Plane ♂ 92	♂ 100	♂ mean	♀ 68	♀ 131	♀ 135	♀ 139	♀ mean	♂ and ♀ mean	High Plane ♂ 69	♂ 132	♂ mean	♀ 143	♀ 95	♀ 101	♀ 138	♀ mean	♂ and ♀ mean
Bone	1917	2368	2143	2244	1710	1799	1901	1915	2032	4390	4771	4580	4949	3816	4274	5037	4519	4550
Muscle	4532	6839	5686	6374	5099	5215	5544	5558	5622	14807	16780	15794	19145	12870	15614	20123	16938	16366
Fat:																		
Subcutaneous	524	930	727	1126	408	448	820	701	714	7970	8380	8175	9226	4722	5806	10151	7476	7826
Intermuscular	370	441	406	423	234	272	468	349	378	2738	3981	3360	4047	1790	1976	4086	2975	3167
Total	894	1371	1133	1549	642	720	1288	1050	1092	10708	12361	11535	13273	6512	7782	14237	10451	10993
Skin	806	1070	938	975	757	749	699	795	867	1923	1807	1865	1709	1703	1918	1890	1805	1835
Tendon, glands, etc.	556	714	635	659	623	612	706	650	643	1138	1449	1299	1418	997	1202	1483	1275	1287
Loss in dissection	234	460	347	352	302	344	275	318	323	1146	455	800	638	391	723	956	678	736
Carcass weight (joints)	8939	12822	10881	12123	9133	9439	10413	10277	10579	34112	37623	35868	41132	26289	31513	43726	35665	35767

Composition of pigs at 16 weeks

Head (g.)

	Low Plane ♂ 92	♂ 100	♂ mean	♀ 68	♀ 131	♀ 135	♀ 139	♀ mean	♂ and ♀ mean	High Plane ♂ 69	♂ 132	♂ mean	♀ 143	♀ 95	♀ 101	♀ 138	♀ mean	♂ and ♀ mean
Total weight	1343	1933	1638	1698	1294	1331	1442	1441	1539	3274	3210	3242	3598	2797	2918	3460	3193	3217
Bones:																		
Tongue	4	4	4	4	4	4	4	4	4	5	7	6	6	11	7	7	8	7
Lower jaw	99	121	110	119	96	102	110	107	109	196	223	210	247	182	213	259	225	217
Skull	306	350	328	336	261	289	305	298	313	630	665	648	749	564	576	748	659	654
Total	409	475	442	459	361	395	419	409	426	831	895	864	1002	757	796	1014	892	878
Muscle	293	497	395	415	313	327	374	357	376	665	675	670	765	578	609	760	678	674
Fat:																		
Subcutaneous	100	140	120	159	23	23	41	62	91	519	323	421	557	414	293	391	414	418 *
Intermuscular	71	82	77	52	40	39	52	46	62	257	247	252	320	152	211	242	231	242
Total	171	222	197	211	63	62	93	108	153	776	570	673	877	566	504	633	645	660

Tongue	71	83	77	81	55	64	58	65	71	116	115	116	119	99	86	118	106	111
Brain	72	83	78	88	86	77	89	85	82	93	90	92	89	92	91	87	90	91
Eyes	9	9	9	10	9	9	8	9	9	9	9	9·5	9·5	9	10	9	9·3	9·4
Ears	105	163	134	135	114	120	146	129	132	232	222	227	221	221	251	221	229	228
Skin	106	149	128	119	70	82	75	87	118	234	149	192	132	221	163	116	158	175
Tendon and waste	98	137	118	111	126	109	112	115	117	128	356	242	277	117	252	326	243	243
Glands	20	28	24	26	23	25	20	24	24	75	39	57	54	62	54	39	52	55
Loss in dissection	+11	87	38	43	74	61	48	59	49	114	90	102	53	75	102	137	92	97
Total weight	691	995	843	1022	790	802	1034	912	877	2666	3721	3199	3964	2140	2648	4326	3270	3235
Neck (g.)																		
Bones: Atlas	18	23	20·5	23	15	17	19	18·5	19·5	40	38	39	42	33	42	44	43	41
Axis	15	19	17	18	15	14	16	16	16·5	33	33	33	35	29	34	36	33·5	33
Cervical	54	72	63	71	50	50	56	57	60	126	131	129	133	108	132	134	127	128
Total	87	114	100	112	80	81	91	91	96	199	202	201	210	170	208	214	201	201
Muscle	413	625	519	568	510	499	610	547	533	1054	1472	1263	1729	970	1243	1818	1440	1352
Fat: Subcutaneous	63	102	82·5	163	55	80	124	106	94	617	956	787	1012	428	583	1155	795	791
Intermuscular	42	45	43·5	76	43	51	98	67	55	395	824	610	741	333	321	846	560	585
Total	105	147	126	241	98	131	222	173	149	1012	1780	1397	1753	761	904	2001	1355	1376
Skin	34	51	42·5	49	52	47	47	49	46	97	163	130	130	111	159	153	138	134
Tendon and glands	23	21	27	15	15	18	26	18·5	23	76	30	53	46	70	50	63	57	55
Loss in dissection	29	37	33	37	35	26	38	34	34	228	74	151	96	57	84	77	79	115
Total weight	1906	2488	2197	2380	1858	1900	1961	2025	2111	6082	6706	6394	6610	4826	5803	7212	6113	6252
Shoulder (2) (g.)																		
Bones: Scapula	68	79	73·5	73	57	69	64	66	70	172	218	195	219	153	182	244	199	197
Humerus	131	168	150	152	128	123	134	134	142	299	341	320	331	262	303	356	313	317
Radius-ulna	100	117	109	105	82	85	90	91	100	211	239	225	230	177	194	240	210	218
Carpals	21	26	23·5	26	20	18	24	22	23	53	58	56	56	44	52	54	52	54
Cannon	28	36	32	34	26	27	30	29	31	63	73	66	73	54	58	71	64	65
Splints	8	10	9	10	9	8	9	9	9	20	21	21	19	15	16	20	18	19
Total leg	356	436	397	400	322	330	351	351	375	818	950	883	928	705	805	985	856	870

APPENDIX III (*continued*)

	Low Plane ♂ 92	♂ 100	♂ mean	♀ 68	♀ 131	♀ 135	♀ 139	♀ mean	♂ and ♀ mean	High Plane ♂ 69	♂ 132	♂ mean	♀ 143	♀ 95	♀ 101	♀ 138	♀ mean	♂ and ♀ mean
							Shoulders (2) (g.) *continued*											
Dew claws (2)	6·3	8·0	7·1	8·0	6·0	6·0	6·0	6·5	6·8	17·3	16·7	17·0	16·6	12·3	14·8	14·6	14·6	15·8
Pasterns (2)	11·4	14·4	12·9	14·6	10·5	10·7	11·0	11·7	12·3	28·1	31·1	29·6	30·5	22·3	26·3	29·1	27·1	28·4
Coronets (2)	6·1	8·7	7·4	8·7	6·0	6·4	6·8	7·0	7·2	16·0	19·3	17·7	18·4	12·9	13·7	18·1	15·8	16·8
Pedals (2)	4·1	6·3	5·2	6·0	4·5	4·0	3·6	4·5	4·9	9·9	12·2	11·1	11·8	8·2	10·1	10·4	10·1	10·6
Navicula and sesamoids (4)	1·5	2·7	2·1	2·7	1·6	2·1	2·1	2·1	2·1	6·1	8·0	7·0	7·8	5·1	6·2	6·9	6·5	6·8
Total foot	29·4	40·1	34·7	40·0	28·6	29·2	29·5	31·8	33·3	77·4	87·3	82·4	85·1	60·8	71·1	79·1	74·1	78·4
Total bone	385	476	431	440	351	359	381	383	407	895	1037	966	1013	766	876	1064	930	948
Muscle:																		
Shoulder	960	1308	1134	1190	987	1031	983	1048	1091	2727	2991	2859	3100	2289	2839	3350	2895	2877
Arm	100	155	128	127	117	116	129	122	125	276	346	311	393	264	307	417	345	328
Cannon	4	10	7	7	7	8	8	8	8	17	20	19	20	11	17	21	17	18
Total	1064	1473	1269	1324	1111	1155	1120	1178	1223	3020	3357	3189	3513	2564	3163	3788	3257	3223
Fat:																		
Subcutaneous	88	135	112	175	62	87	108	108	110	1098	1136	1117	988	687	767	1264	926	1022
Intermuscular (shoulder)	80	78	79	93	51	44	69	64	72	412	552	482	486	266	330	438	380	431
Intermuscular (arm)	20	11	15	14	6	7	7	8·5	12	52	34	43	37	21	36	28	31	37
Total intermuscular	100	89	94	107	57	51	76	73	84	464	586	525	523	287	366	466	411	468
Total fat	188	224	206	282	119	138	184	181	194	1562	1722	1642	1511	974	1133	1730	1337	1490
Skin	186	208	197	179	171	158	160	167	182	344	344	344	295	308	367	329	325	335
Tendon, glands, etc.	59	51	55	76	59	51	75	65	60	150	201	176	196	138	150	213	174	175
Loss in dissection	24	56	40	79	47	39	41	52	46	111	45	78	76	76	114	88	91	85
							Thorax (g.)											
Total weight	1818	2823	2321	2607	1802	1938	2135	2121	2221	8715	9187	8951	11298	6169	7486	11834	9197	9074
Bones:																		
Ribs and sternum	248	302	275	263	178	198	214	213	244	564	595	580	626	498	550	640	579	580
Vertebrae	169	235	202	229	170	165	174	185	194	421	430	426	456	347	392	453	412	419
Total	417	537	477	492	348	363	388	398	438	985	1025	1006	1082	845	942	1093	991	998

	3912	4140	496	3714	2951	4927	3683	3902	3463	1277	1217	1204	1113	1110	1442	1337	1628	1046
Muscle																		
Fat: Subcutaneous	2264	2262	3144	1646	1240	3017	2265	2205	2325	158	160	196	90	95	257	155	212	98
Intermuscular	1227	1156	1742	640	590	1653	1297	1465	1128	79	81	119	57	39	111	77	97	57
Total	3491	3418	4886	2286	1830	4670	3562	3670	3453	237	241	315	147	134	368	232	309	155
Skin	430	442	508	441	378	440	428	408	447	197	177	150	157	156	245	216	253	178
Tendon, glands, etc.	21	23	18	35	16	22	19	20	18	14	15	14	12	11	22	12	13	10
Loss in dissection	220	184	362	68	149	157	256	162	349	61	73	64	146	43	38	48	83	12
Total weight	3675	3606	4460	3117	2461	4384	3744	3839	3648	816	818	929	759	770	814	814	1005	622
Bones: Vertebrae	252	250	265	245	217	271	254	251	257	109	105	104	100	103	111	112	127	97
Loin (g.)																		
Muscle: Loin	1405	1468	1739	1307	1082	1743	1341	1377	1305	389	403	453	371	378	410	375	465	285
Psoas	393	401	491	364	279	472	385	415	355	111	111	126	112	103	103	111	133	88
Total	1798	1869	2230	1671	1361	2215	1726	1792	1660	500	514	579	483	481	513	486	598	373
Fat: Subcutaneous	1107	975	1359	749	526	1266	1238	1212	1264	70	71	102	48	58	75	69	98	39
Intermuscular	223	221	303	149	111	322	225	303	146	26	22	36	22	14	16	29	35	23
Total	1330	1196	1662	898	637	1588	1463	1515	1410	96	93	138	70	72	91	98	133	62
Skin	236	224	230	251	201	214	248	229	266	84	85	87	84	84	85	83	98	68
Tendon, glands, etc.	14	16	16	13	22	12	12	12	11	13	8	7	7	7	11	17	22	12
Loss in dissection	47	51	57	39	23	84	42	40	44	17	14	14	15	23	3	10	27	10
Total weight	3111	2973	3427	3205	2401	2860	3249	3270	3228	775	760	731	647	626	1037	790	882	697
Pelvis (g.)																		
Bones: Pelvis	250	254	287	242	220	268	245	255	235	101	96	93	96	81	115	107	114	99
Sacrum	77	79	83	91	65	77	74	83	65	34	34	34	32	23	45	33	36	30
Tail vertebrae	14	15	21	13	10	16	13	13	14	5	3	4	2	3	5	6	6	7
Total	341	348	391	346	295	361	332	351	314	140	133	131	130	107	165	146	156	136
Muscle	1258	1246	1344	1370	1066	1202	1270	1237	1303	400	404	352	355	317	591	397	464	330
Fat: Subcutaneous	1037	934	1191	995	647	905	1140	1149	1131	76	89	110	47	65	135	62	76	47
Intermuscular	178	151	194	109	153	146	204	262	145	26	19	36	16	13	10	32	29	35
Total	1215	1085	1385	1104	800	1051	1344	1411	1276	102	108	146	63	78	145	94	105	82
Skin	173	174	178	223	168	125	171	165	177	66	66	52	56	66	88	66	77	55
Tendon, tail, etc.	69	60	50	84	39	65	78	64	92	27	26	22	27	26	30	28	37	20
Loss indissection	61	67	79	78	33	56	54	42	66	42	24	28	16	32	18	59	43	74

APPENDIX III (continued)

Legs (2) (g.)

	Low Plane									High Plane								
	♂ 92	♂ 100	♂ mean	♀ 68	♀ 131	♀ 135	♀ 139	♀ mean	♂ and ♀ mean	♂ 69	♂ 132	♂ mean	♀ 143	♀ 95	♀ 101	♀ 138	♀ mean	♂ and ♀ mean
Total weight	1862	2696	2279	2565	1993	2062	2181	2200	2240	6499	7690	7095	8418	5495	6336	9007	7314	7203
Bones:																		
Femur	145	179	162	176	138	143	145	151	156	332	369	351	370	284	328	372	339	345
Tibia-fibula	111	129	120	124	94	102	103	106	113	239	277	258	276	211	240	279	252	255
Patella	8	11	9·5	11	8	8	8	9	9	23	21	22	22	18	20	20	20	21
Calcaneum	22	28	25	26	20	20	23	22	24	56	58	57	57	46	46	58	52	54
Astragalus	21	29	25	28	22	22	25	24	25	52	56	54	57	40	44	50	47	50
Tarsals	14	19	16·5	19	14	13	16	15·5	16	42	46	44	46	32	34	40	38	41
Cannons	31	40	35·5	37	30	30	32	32	34	74	82	78	84	61	67	80	73	75·5
Splints	7	8	7·5	8	6	6	7	6·5	7	16	18	17	17	13	15	17	15	17
Total leg	359	443	401	429	332	344	359	366	384	834	927	881	926	705	794	916	835	858
Dew claws (2)	4·7	7·0	5·9	5·5	4·6	4·5	4·6	4·8	5·4	13·7	14·0	13·9	14·4	10·2	11·5	13·8	12·5	13·2
Pasterns (2)	10·9	15·2	13·1	14·7	11·3	10·4	11·2	11·9	12·5	29·1	31·8	30·5	33·2	23·9	26·9	31·8	28·9	29·7
Coronets (2)	5·9	8·7	7·3	8·5	5·5	5·9	6·7	7·0	7·0	17·4	19·3	18·4	20·4	13·7	14·6	19·0	16·9	17·7
Pedals (2)	3·9	6·5	5·2	5·2	4·5	4·2	3·4	4·3	4·8	9·2	11·3	10·2	11·8	8·2	8·8	10·3	9·8	10·0
Navicula and sesamoids (4)	2·0	2·7	2·4	2·3	2·1	1·5	1·9	2·0	2·2	5·4	6·3	5·9	6·6	4·6	5·2	6·2	5·7	5·8
Total foot	27·4	40·1	33·9	36·2	28·0	26·5	27·8	29·6	31·7	74·8	82·6	78·7	86·4	60·6	67·0	81·1	73·8	76·3
Total bones	386	483	435	465	360	370	387	396	416	909	1010	960	1012	766	861	997	908	934
Muscle:																		
Thigh	833	1296	1065	1270	1044	1069	1076	1115	1090	3068	3590	3329	3976	2830	3168	4323	3574	3452
Leg	182	247	215	241	203	204	219	217	216	547	724	636	779	530	652	860	705	671
Cannon	7	11	9	10	10	10	10	10	10	27	31	29	33	20	24	33	28	29
Total	1022	1554	1289	1521	1257	1283	1305	1342	1315	3642	4345	3994	4788	3380	3844	5216	4307	4152
Fat:																		
Subcutaneous	89	167	128	160	50	73	139	106	117	1016	1399	1207	1481	780	773	1647	1170	1189
Intermuscular (thigh)	29	46	37·5	38	20	26	40	31	34	169	242	206	284	126	138	249	199	203
Intermuscular (leg)	13	18	15·5	13	8	10	11	10·5	13	34	52	43	58	38	42	44	46	44
Total intermuscular	42	64	53	51	28	36	51	41	47	203	294	249	342	164	180	293	245	247
Total fat	131	231	181	211	78	109	190	147	164	1219	1693	1456	1823	944	953	1940	1415	1436
Skin	179	234	207	210	158	165	128	165	186	358	349	354	373	316	314	376	445	400
Tendon, glands, etc.	48	67	58	54	92	93	129	92	75	137	291	214	308	111	126	323	217	216
Loss in dissection	96	127	112	104	48	41	42	59	86	234	2	118	116	+22	238	156	122	120

Organs and offals (g.)

Empty live weight	47014	46467	56348	41849	35013	52657	47561	49032	46090	14640	13966	14173	12780	12590	16320	15315	18285	12345
Skin and hair	497	461	465	512	366	502	532	592	472	271	261	281	259	238	268	275	284	265
Hoofs: Fore	24	24	29	23	17	27	24	28	20	7·0	8·5	8	8	8	10	9·5	11	8
Hind	18·5	18·5	23	15	15	21	18·6	21	16	7·0	7·0	7	7	7	7	7·0	8	6
Blood: Total	2788	2800	2775	2546	2902	2978	2776	2782	2770	944	908	933	880	836	982	980	1290	670
Neck thymus	100	118	148	106	105	112	82·5	97	66	14	13	15	10	12	14	15	10	20
Heart thymus	33	35	40	30	30	38	32	42	22	7·5	6·5	6	4	6	10	8·5	9	8
Lymphatics and salivary	108	117	117	135	122	95	99·5	90	109	68	65	51	86	68	56	71	70	72
Total glands	241	270	305	271	257	245	214	229	197	89·5	84·5	72	100	86	80	94·5	89	100
Diaphragm	224	235	314	198	168	260	213	231	195	76	73	82	65	63	83	79·5	99	60
Heart	180	190	212	171	156	222	171	177	165	73	65	75	56	57	71	81	97	65
Pericardium and blood vessels	125	149	152	137	79	227	101	127	75	44	40	55	35	38	33	48	66	30
Lungs and trachea	465	465	500	489	421	450	464	451	477	224	201	207	192	205	200	247	293	201
Thoracic organs	994	1039	1178	995	824	1159	949	986	912	417	379	419	348	363	387	455	555	356
Oesophagus	35	35	37	34	32	36	35	33	37	21	19·5	19	17	18	24	23	27	19
Stomach	332	353	377	379	328	327	311	267	355	186	180	205	167	148	200	192	237	148
Small intestine	1265	1204	1299	1215	1121	1180	1326	1272	1380	576	539	614	470	520	550	612	790	435
Caecum	90	90	94	93	91	82	90	75	106	43	34	30	30	32	45	52	56	47
Large intestine	508	470	518	409	442	511	545	450	640	245	221	229	182	188	285	269	335	203
Rectum	137	112	130	113	105	100	161	132	190	62	52	47	51	44	65	72	80	64
Total tract	2367	2264	2455	2243	2119	2236	2468	2229	2708	1133	1045	1144	917	950	1169	1220	1525	916
Caul	45	51	75	31	28	70	40	49	32	5·5	5·25	6	4	6	5	6	8	4
Mesentery	517	532	720	440	322	645	503	585	420	124	133	153	120	132	127	115	136	94
Liver	1624	1494	1795	1318	1287	1578	1753	1541	1965	558	516	577	426	542	520	599	778	419
Gall bladder	30·5	28	34	43	22	12	32	21	44	5·4	3·25	4	16	17	1	7·5	9	6
Spleen	52	57	66	53	45	65	47·5	45	50	23	19·5	23	36	23	21	26·5	33	20
Pancreas	105	98	125	78	70	121	112	116	107	32·5	32·5	33	36	64	38	32·5	36	29
Kidneys	283	250	312	225	186	276	315	319	310	69	69·5	66	73	64	74	69·5	102	37
Leaf and kidney fat	508	492	840	282	212	634	524	584	464	34·5	37·5	60	28	30	32	31·5	40	23
Bladder	25·5	28	37	26	21	30	22·5	25	20	13·5	12·5	12	11	12	15	14·5	14	15
Total abdominal	5556	5294	6459	4739	4312	5667	5817	5514	6120	1998	1874	2078	1635	1780	2002	2122	2681	1563
Uterus and vagina or	124	124	161	110	94	132	—	—	—	18	18	17	19	20	17	—	—	—
Penis and vesicula seminalis	59·5	—	—	—	—	—	59·5	70	49	28·5	—	—	—	—	—	28·5	38	19
Total offals	10210	10031	11395	9211	8787	10731	10389	10222	10556	3757	3540	3815	3256	3338	3753	3971	4956	2987

APPENDIX III (continued)

Length of alimentary tract (cm.)

	Low Plane									High Plane								
	♂ 92	♂ 100	♂ mean	♀ 68	♀ 131	♀ 135	♀ 139	♀ mean	♂ and ♀ mean	♂ 69	♂ 132	♂ mean	♀ 143	♀ 95	♀ 101	♀ 138	♀ mean	♂ and ♀ mean
Small intestine	1380	1512	1446	1387	1455	1536	1633	1503	1475	1869	2194	2032	1728	1905	1873	2004	1877	1954
Caecum	14	16	15	15	15	13	15	14·5	15	20	19	19·5	19	20	22	23	21	20·5
Large intestine	155	191	173	210	175	172	243	200	187	258	270	264	273	226	254	288	260	262
Rectum	89	90	90	85	72	90	88	84	87	137	119	128	91	107	103	109	103	115·5
Total length	1638	1809	1724	1697	1717	1811	1979	1801	1764	2284	2602	2443	2111	2258	2252	2424	2261	2352

Body and carcass measurements at 16 weeks

Carcass measurements (mm.)

	Low Plane									High Plane								
	♂ 92	♂ 100	♂ mean	♀ 68	♀ 131	♀ 135	♀ 139	♀ mean	♂ and ♀ mean	♂ 69	♂ 132	♂ mean	♀ 143	♀ 95	♀ 101	♀ 138	♀ mean	♂ and ♀ mean
Body length:																		
Head	29	29	29	27	27	26	29	27	28	31	34	33	35	33	35	31	34	34
Neck	73	69	71	79	80	95	101	89	80	112	141	127	146	91	91	166	124	126
Thorax	254	352	303	307	277	260	268	278	290	394	388	391	408	375	395	380	390	391
Loin	122	129	126	123	142	135	150	138	132	188	187	185	210	180	162	200	188	188
Pelvis	124	123	124	142	107	89	118	114	119	149	161	155	155	143	191	174	166	160
Total length	598	710	654	659	628	617	672	644	649	868	910	889	954	799	883	960	899	894
Carcass:																		
Length of side	430	488	459	501	452	441	475	467	463	635	642	639	703	595	620	697	654	647
Length of leg	350	375	363	404	365	366	385	380	372	493	501	497	520	470	465	515	493	495
Depth of rib	180	196	188	198	171	174	183	182	185	275	275	275	283	252	258	299	273	274
Forearm length	123	133	128	149	140	132	145	142	135	183	191	187	190	171	165	190	179	183
Forearm circumference	133	140	137	130	120	119	132	125	131	175	202	189	209	185	190	216	200	195
Circumference base of tail	39	55	47	62	56	47	45	53	50	65	71	68	77	65	83	72	74	71
Foretrotter	65	68	67	76	62	63	61	66	67	86	86	86	84	86	86	84	85	86

Streak:																		
Breast	11·0	12·0	11·5	11·5	9·0	9·5	11·0	10·3	10·9	18·0	23·0	20·5	29·0	22·0	19·0	26·0	24·0	22·2
Middle	11·5	8·0	9·8	10·0	10·0	10·5	10·0	10·1	10·0	21·0	24·0	22·5	29·0	20·0	20·0	25·0	23·5	23·0
Inguinal	7·5	6·5	7·0	8·0	4·5	5·0	8·0	6·4	6·7	22·0	24·0	23·0	25·0	20·0	20·0	28·0	23·3	23·2
Back fat:																		
Shoulder: Inner	4	8	6	7	7	3	8	6·3	6·2	22	28	25	30	22	20	35	26·8	25·9
Outer	3	5·5	4·3	6	3	3	2	3·5	3·9	6	5	5·5	6	5	7	6	6·0	5·8
Loin: Inner	0·5	2	1·25	2	0·5	0·5	1	1·0	1·1	9·5	5	7·3	10	5	5	11	8·0	7·7
Outer	0·5	1	0·75	1	0·5	0·5	1	0·8	0·8	5	5	5·0	5	4	4	5	4·5	4·7
Rump: (1)	1·0	4·5	2·8	3·0	2·0	1·0	1·0	1·8	2·3	29·0	21·0	25·0	25·5	17·5	17·5	29·5	21·5	23·3
(2)	1·0	2·0	1·5	3·0	1·0	1·0	1·0	1·5	1·5	17·0	16·0	16·5	11·5	8·0	10·0	18·0	11·9	14·2
(3)	1·0	3·5	2·3	3·0	2·0	1·0	2·0	2·0	2·2	26·0	22·0	24·0	20·0	9·5	15·0	23·5	17·0	20·5
Mean rump	1·0	3·3	2·2	3·0	1·7	1·0	1·3	1·8	2·0	24·0	20·0	22·0	19·0	10·3	14·1	23·7	16·8	19·4
Mean back fat	3·0	6·6	4·8	6·3	4·2	2·7	4·3	4·4	4·6	22·2	21·0	21·6	23·3	15·4	16·5	27·0	20·6	21·1
Loin cut: A	50	66	58	62	57	53	56	57	58	70	68	69	70	64	73	69	69	69
B	11	16	13·5	19	14	15·5	18	16·6	15·0	30	32	31	40	28	32	38	34·5	32·8
C	1·0	2·5	1·8	2·5	1	1	1·5	1·5	1·6	15·5	13	14·3	13·5	7·5	11	14	11·5	12·9
H	1·5	4·0	2·8	3·0	1	1	2·0	1·8	2·3	25	21	23	20	11	15·5	21	16·9	20·0
Shape index	222	242	232	298	246	292	321	289	260	429	470	450	571	441	438	550	500	475
Thickness of skin	2·5	3·0	2·8	3·0	2·0	2·0	2·0	2·3	2·5	2·0	3·0	2·5	2·0	2·5	2·5	2·0	2·3	2·4
Muscle colour:																		
Diaphragm	10 (beef)	10 (beef)	10 (beef)	9 (beef)	10 (beef)	9 (beef)	5 (pork)	—	—	5 (pork)	10 (beef)	—	4 (pork)	10 (beef)	5 (pork)	5 (pork)	—	—
Loin (pork scale)	5	5	5	4	5	5	5	4·8	4·9	3	5	4	4	2	4	3	3·3	3·6

APPENDIX III (continued)

Weekly live weights (lb.)—16 week series

Pig no.	Birth	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
											Age (weeks)						
								High Plane									
69	3	6¼	11	15	19	23	27	34	40	48	56	65	75	85	94	105	113
95	2¼	6¼	9½	12½	15½	19½	22	25	29	34	39	47	52	60	70	80	87
101	2¼	7	10	13	16	19	22	28	33	46	49	57	65	76	83	93	100
138	2¼	6¼	11	15	19	25	33	42	52	60	68	78	86	99	111	124	132
143	2¼	6¼	10	15	19	24	30	39	48	54	63	72	84	92	105	117	126
132	2¼	6	9	12	17	22	26	33	41	47	53	59	69	79	94	108	120
Mean	2⅜	6¼	10	13·7	17·6	22·0	26·7	33·5	40·5	47·0	54·7	63·0	72·0	82·0	93·0	104·5	113·0
								Low Plane									
68	2¼	5¼	9	12	15	18	22	24	26	28	30	33	34	37	40	41	42¼
92	2¼	5	7	7¼	8½	9¼	11	14	16	19	21	24	26	28	30	31	31½
100	2¼	6	8	9	11	12	15	21	25	27	29	31	32	35	38	42	47
131	2¼	5	8	10	12	13	16	17¼	19¼	21	23	24¼	26	27¼	28	30	32
135*	2¼	5	7	10	11	13	16	17¼	19	21	24	26	28	28	29	31	32
139	3	5¼	8	11	12	13	15	17	19	20	21	24	26	28	30	34	37
Mean	2·6	5·4	7·8	9·7	11·5	13·1	16·0	18·5	20·7	22·7	24·7	27·1	28·7	30·6	32·5	35·0	37·0

High (below) and Low (above) Plane pigs at 16 weeks.—Same scale.

Body proportions at 16 weeks.

Body proportions at 16 weeks.

KIDNEYS AT SIXTEEN WEEKS
HIGH PLANE   LOW PLANE
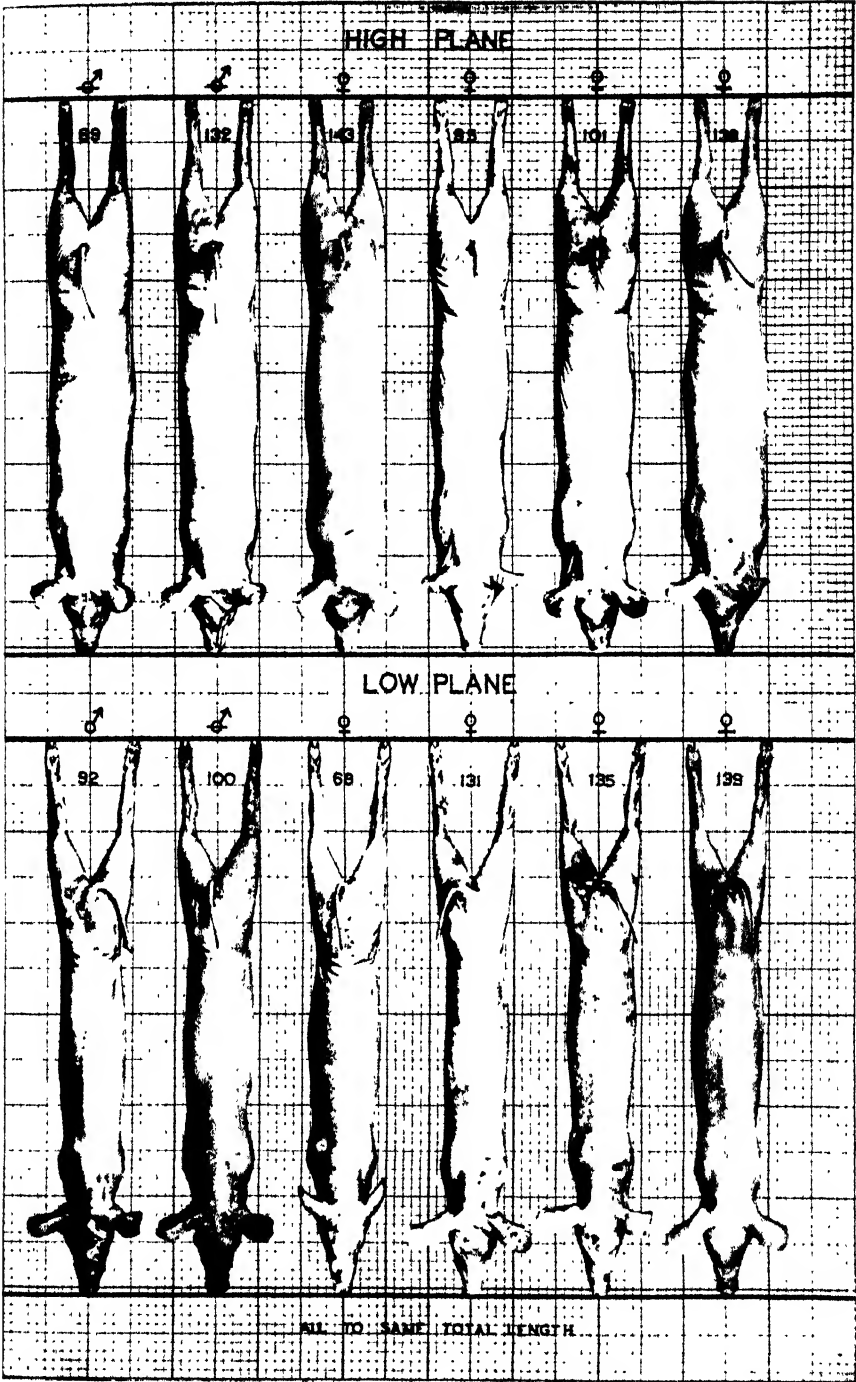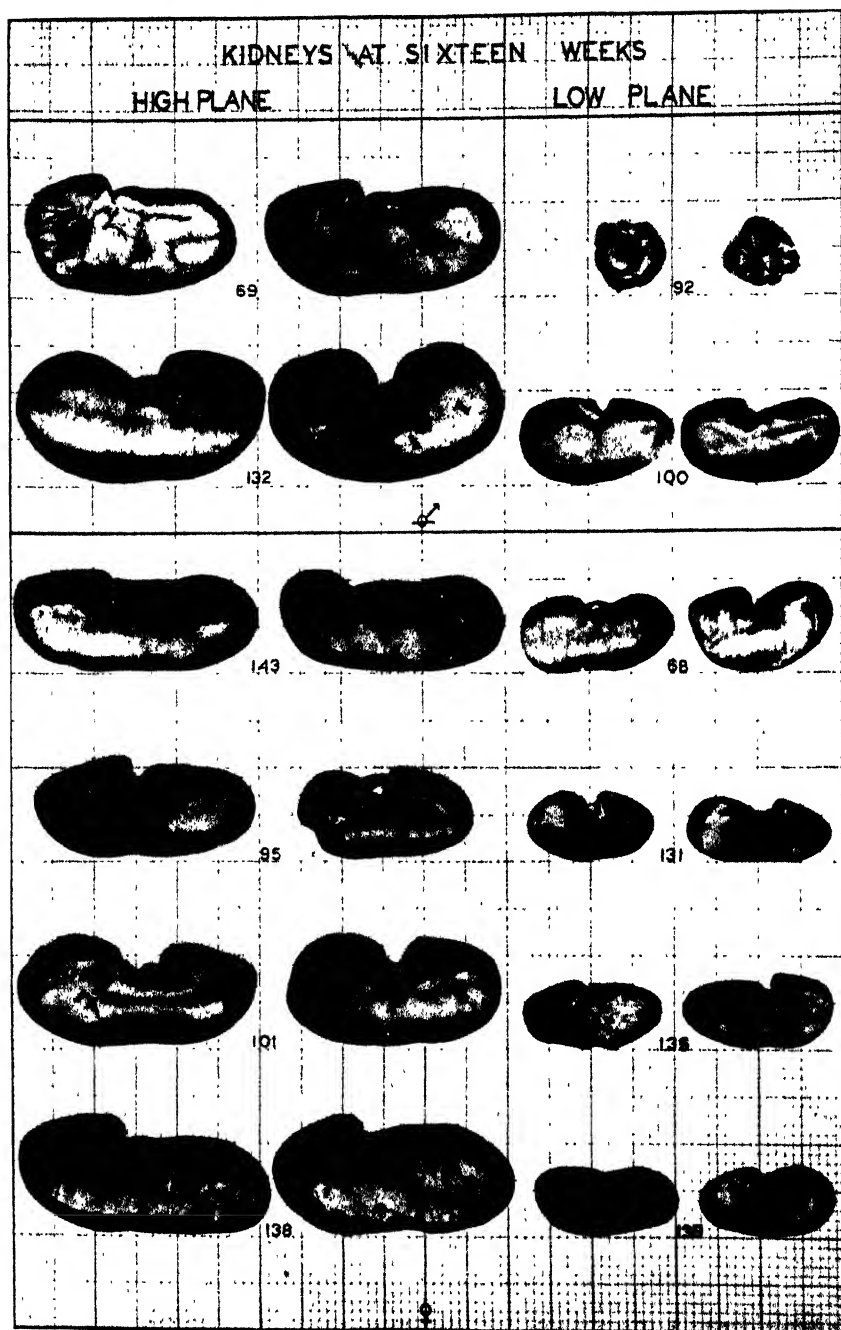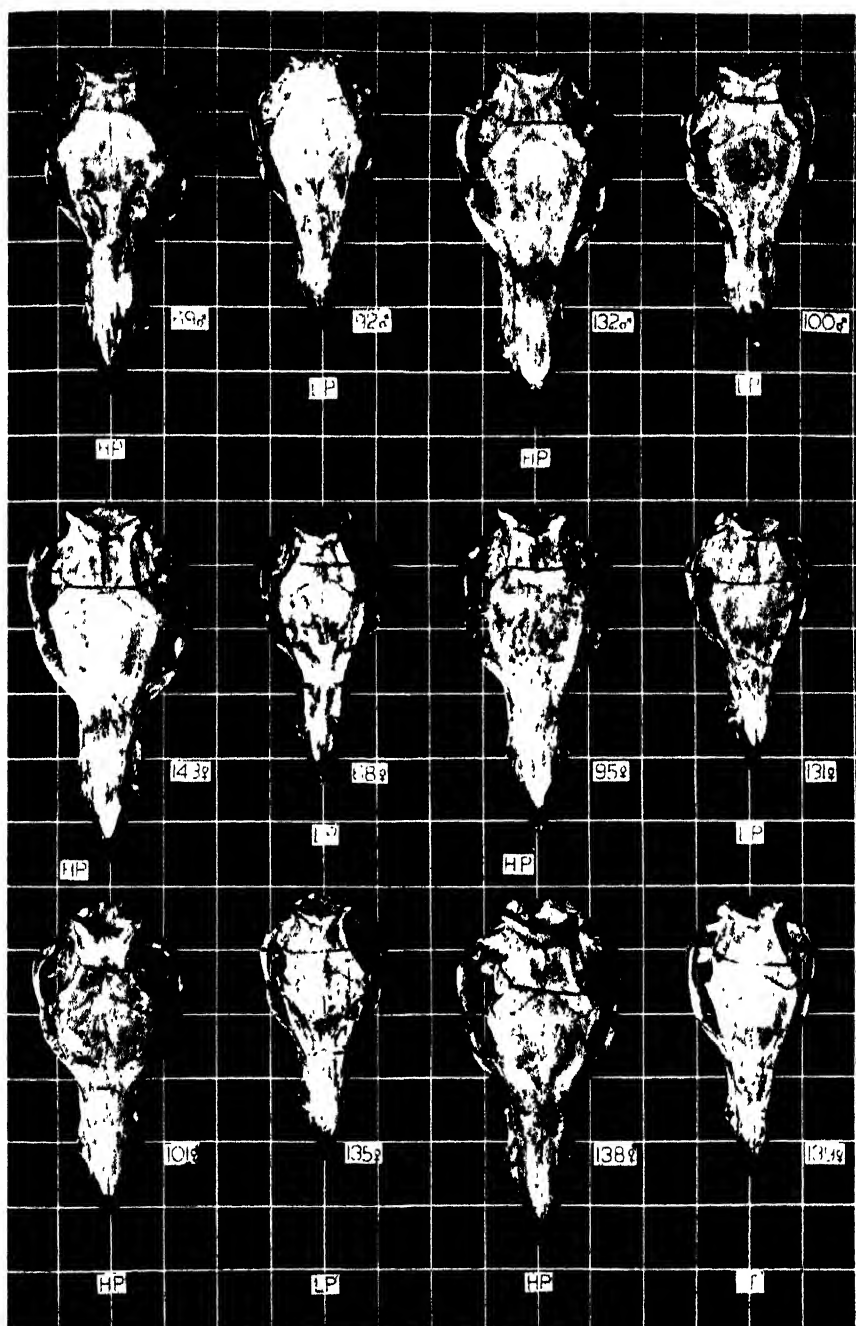
Skulls. Effect of plane of nutrition on development of bone at 16 weeks.
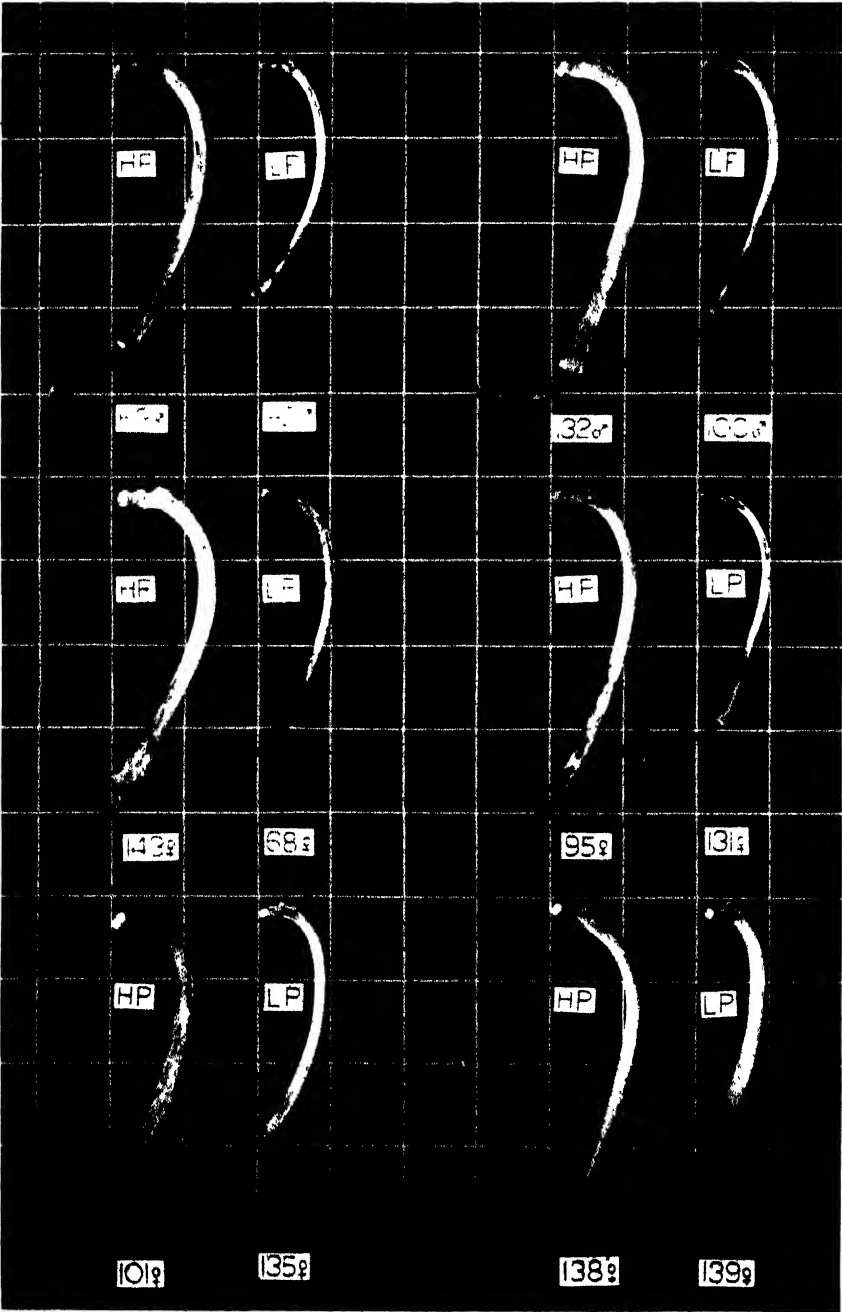
Sixth rib. Effect of plane of nutrition on development of bone at 16 weeks.

Lumbar vertebrae. Effect of plane of nutrition on development of bone at 16 weeks.

Pelvis. Effect of plane of nutrition on development of bone at 16 weeks

[Femur　Effect of plane of nutrition on development of bone at 16 weeks

Hind cannons (metatar-al-). Effect of plane of nutrition on development of bone at 16 weeks.

LOIN CUT AT LAST RIB AT SIXTEEN WEEKS

HIGH PLANE

LOW PLANE

ALL TO SAME EYE MUSCLE LENGTH
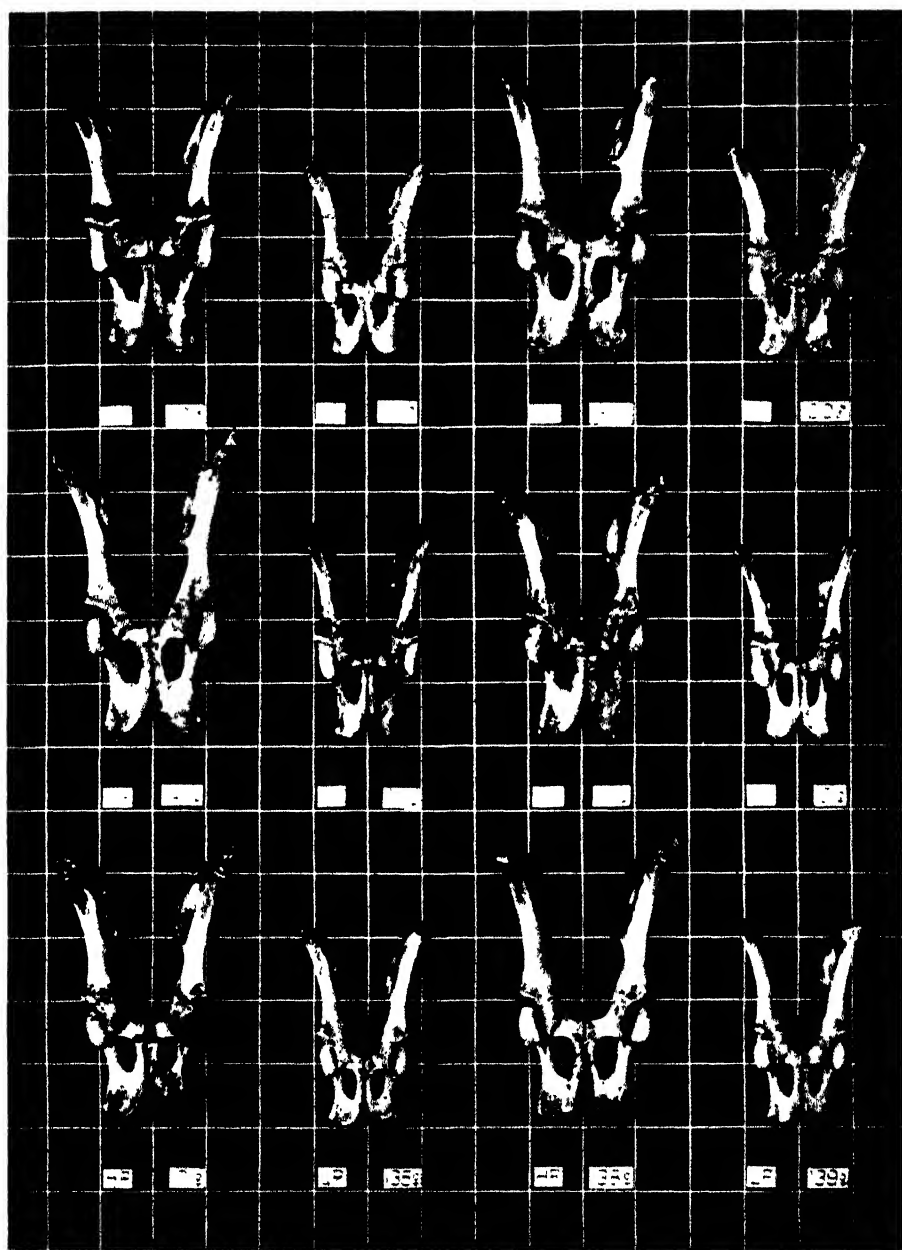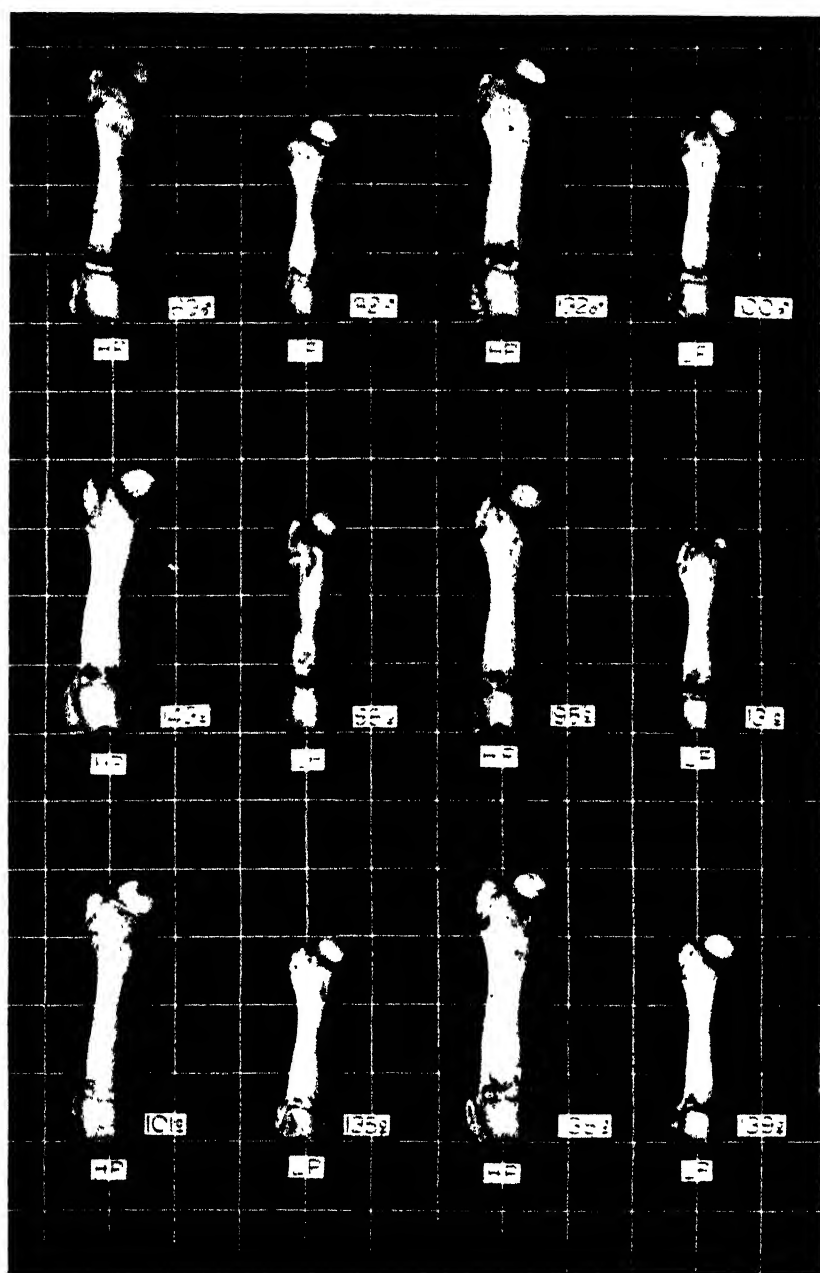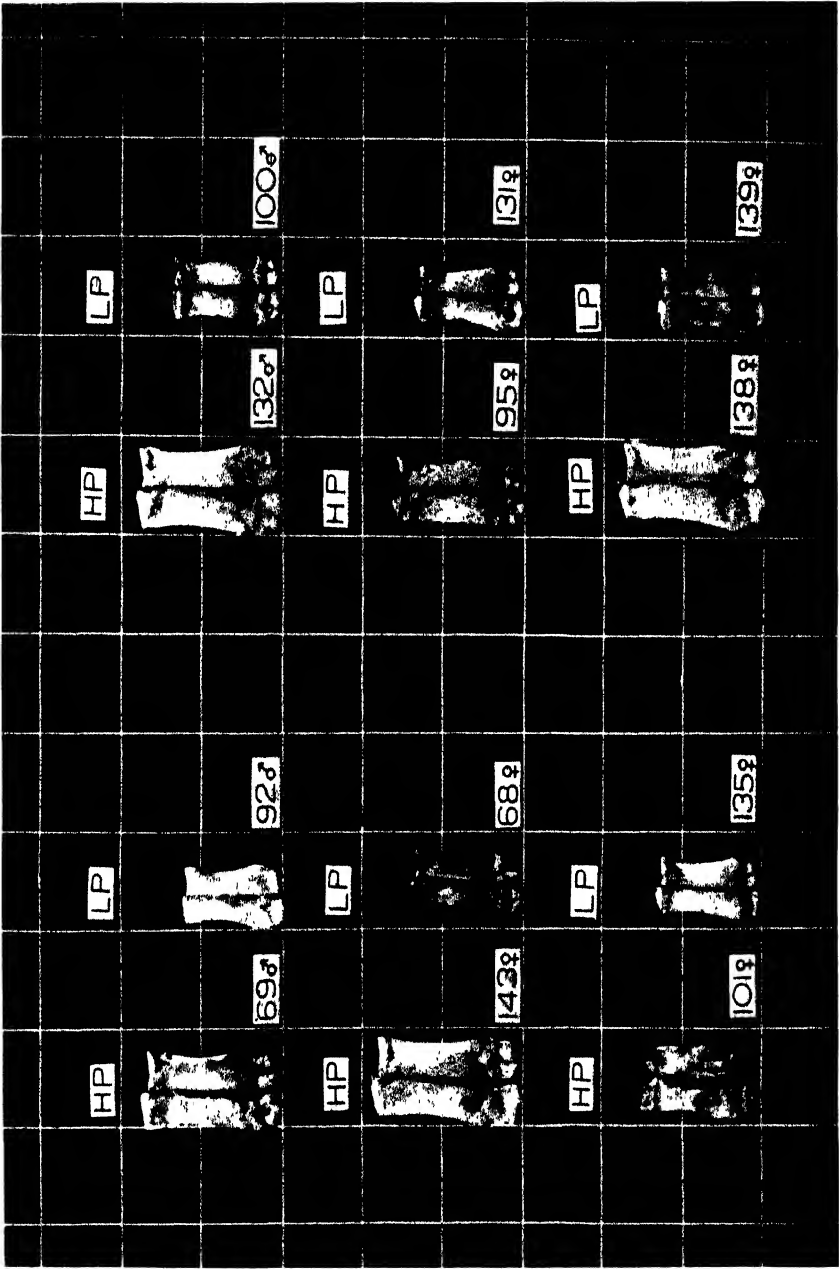
GAS AND VAPOUR MOVEMENTS IN THE SOIL

I. THE DIFFUSION OF VAPOURS THROUGH POROUS SOLIDS

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(With Five Text-figures)

THE greater part of the research work on soils is, and has been, understandably devoted to the properties of the solid and liquid parts of the soil system, and a survey of the literature shows that the attention paid to the physics of the soil atmosphere is much less than its biological importance deserves. Physically, the most important problem associated with the soil atmosphere is the investigation of the mechanism of gas and vapour movements in the soil, such as the gaseous exchange of oxygen from the outside atmosphere for the carbon dioxide being produced in the neighbourhood of plant roots or by micro-organisms in the soil. Keen (1931) has provided a survey of this problem based on the work of Romell (1922) and Buckingham (1904), and shows that whilst changes in the soil temperature, changes in the barometric pressure, and the effects of wind, rain and evaporation may all assist in the process, gaseous diffusion provides the only continuously operating mechanism capable of accounting quantitatively for the observed gas movements. The numerical calculations of the rate of exchange depend on Buckingham's finding that the rate of diffusion of a gas through a porous solid is approximately proportional to the square of the porosity (fractional part of the system not occupied by solid or liquid) and is independent of the moisture content and texture of the soil. His experimental points show a large scatter and the parabolic law can be regarded as a first approximation only. In an endeavour to obtain a more precise relation, Smith & Brown (1933) repeated Buckingham's experiments but found, with their moist field soils, that reliable diffusion coefficients were unobtainable because of the evolution of carbon dioxide by micro-organisms in the test samples, and it is possible that Buckingham's results were similarly influenced. As the dependence of the rate of diffusion upon porosity is of considerable importance to the plant

physiologist a re-examination of the question needs little justification, and the results will be of interest in other problems. For instance, in using soil fumigants the spreading of the toxic vapour is primarily a diffusion process, and knowledge of the diffusion-porosity law will enable the optimum depths, spacings and quantities of injection to be forecast to achieve a required space-time distribution of vapour. Some empirical data on the spreading of carbon disulphide vapour have been obtained by Higgins & Pollard (1937), and although their experimental conditions involve complex boundary conditions in the mathematical analysis, it has been possible to make reasonable simplifying assumptions and to show that an adequate description of their results can be obtained by considering the vapour movement as diffusion.

The reduced rate of diffusion through a porous body is due in part to the reduced area of cross-section available for gas movements and in part to the increased path length imposed by the tortuous nature of the channels which the molecules must follow. We should thus expect, for a given porous solid, that the relation between the steady state rate of diffusion and porosity will be the same for all gases and vapours and may be expressible in the form $D = D_0 f(S)$, where D is the coefficient of diffusion through a material of pore-space S, and D_0 is the coefficient of diffusion through free air $(S = 1 \cdot 0)$. In Buckingham's equation, $f(S) = S^2$.

Acceptance of this general law enables a considerable simplification of the experimental technique to be made. Instead of using a gas such as carbon dioxide, necessitating complex arrangements for producing and maintaining a known partial pressure on one face of a soil sample, and some means, either chemical or physical, for estimating the rate of flow through the sample, a vapour such as carbon disulphide or acetone can be used, the rate of evaporation of the liquid being measured by direct weighing. The partial pressure gradient is readily obtained, because the pressure difference across the faces of the soil sample is merely the saturated vapour pressure of the liquid at the temperature of the experiment. After a preliminary experiment the dimensions of the apparatus necessary to give reasonable accuracy in all measurements which must be made are readily determined. A description of the apparatus appears below (p. 446).

The present report includes a study of the dependence of D upon S for steady state conditions and also an account of preliminary work on the effects of moisture and adsorption in the non-steady state. The effects of chemical and biological action are not considered.

THEORETICAL

Steady state conditions. If the partial pressures of a diffusing gas be maintained at values p_1 and p_2 at two parallel planes distance l apart in air, the total pressure being uniform throughout the system, there is a steady flow of gas in one direction and an equal flow of air in the opposite direction. If the area of cross-section is A the rates of flow are given by

$$\frac{dq}{dt} = \alpha A \frac{p_1 - p_2}{l},$$

where α is a constant for a given pair of gases. It is a coefficient of diffusion, in units which depend upon those of the other quantities. Measuring A and l in cm., p in mm. of mercury, q in mg. and t in seconds, we may write $\alpha = D_0/\beta$, where β is a constant given by the equation $n = p/\beta$, n being the concentration in mg./c.c. at pressure p. The steady state equation may thus be written in two forms

$$\frac{\partial q}{\partial t} = -\frac{D_0}{\beta} A \frac{\partial p}{\partial l} \qquad .$$

or
$$\frac{\partial q}{\partial t} = -D_0 A \frac{\partial n}{\partial l}, \tag{1}$$

and is true for all planes normal to the direction of flow.

Note that D_0 is the coefficient obtained when n is measured in units of q per c.c.

Non-steady state conditions. When there is not a uniform pressure gradient, equation (1) holds at all planes. Consider two planes δx apart. The amount entering the element at the first is given by

$$\frac{\partial q_1}{\partial t} = -\frac{D_0}{\beta} A \frac{\partial p}{\partial x},$$

the amount leaving at the second is

$$\frac{\partial q_2}{\partial t} = -\frac{D_0}{\beta} A \left\{ \frac{\partial p}{\partial x} + \frac{\partial}{\partial x} \left(\frac{\partial p}{\partial x} \right) \delta x \right\},$$

and the net gain in the element

$$\frac{\partial q}{\partial t} = \frac{D_0}{\beta} A \frac{\partial^2 p}{\partial x^2} \delta x.$$

If n is the concentration, we have $n = q/A\delta x$, i.e. $q/A\delta x = p/\beta$ and we obtain

$$\frac{\partial p}{\partial t} = D_0 \frac{\partial^2 p}{\partial x^2}. \tag{2}$$

The extension to a three-dimensional case yields

$$\frac{\partial p}{\partial t} = D_0 \left\{ \frac{\partial^2 p}{\partial x^2} + \frac{\partial^2 p}{\partial y^2} + \frac{\partial^2 p}{\partial z^2} \right\} = D_0 \nabla^2 p. \tag{2a}$$

Equation (2), or its more general form (2a), formally defines the coefficient of diffusion D_0. The equation is the same as that for the flow of heat in a conducting solid if we replace p by θ, the temperature at any point, and the solution of the diffusion equation in the various practical cases which are presented will follow the same lines as the analogous problems in heat conduction, most of which are adequately dealt with in text books on Fourier analysis.

Diffusion through a porous solid. When the inter-diffusion of gas and air is restricted to movement through the pores of a solid body, the amount of material which can pass across a given plane is reduced because of the smaller area of the cross-section available, and effective pressure gradients are reduced because of the tortuous nature of the paths which the gas molecules must take. Let us define the coefficient of diffusion, D, for a solid of porosity S, in terms of the steady state transfer of mass, by the equation

$$\frac{\partial q}{\partial t} = -\frac{D}{\beta} A \frac{\partial p}{\partial x}. \tag{3}$$

For the non-steady state we obtain

$$\frac{\partial q}{\partial t} = \frac{\partial q_1}{\partial t} - \frac{\partial q_2}{\partial t} = \frac{D}{\beta} A \frac{\partial^2 p}{\partial x^2} \delta x.$$

In this case the quantity q is present in volume $A\delta x S$, i.e.

$$\frac{q}{A\delta x S} = \frac{p}{\beta}$$

and

$$\frac{\partial q}{\partial t} = \frac{A\delta x S}{\beta} \frac{\partial p}{\partial t},$$

i.e.

$$\frac{\partial p}{\partial t} = \frac{D}{S} \frac{\partial^2 p}{\partial x^2}. \tag{4}$$

From equations (3) and (4) an important distinction is established which must be borne in mind when discussing "rate of diffusion". The rate of redistribution of mass is dependent on D (equation (3)); the rate of redistribution of pressure is dependent upon D/S (equation (4)). The above derivation implicitly assumes that the porous solid is isotropic, i.e. that the pore-space is randomly distributed and that in any area of cross-section the fraction not occupied by solid will be S. This will probably be true for most granular solids whose particles approximate

to spheres, i.e. we expect equations (3) and (4) to hold for most soils and sands but anticipate that they will break down for laminated solids such as mica. If the total area of cross-section of the solid is A, the effective area across which diffusion takes place is SA. The effective path length through the solid will be greater than l: let it be l_e. Then in the steady state we may consider the diffusion through a solid of length l and cross-section A as being the same as that through a column of air of length l_e and area SA, i.e. we have

$$\frac{dq}{dt} = \frac{D}{\beta} A \frac{p_1 - p_2}{l}$$

$$= \frac{D_0}{\beta} A S \frac{p_1 - p_2}{l_e}$$

or

$$D = D_0 S \frac{l}{l_e}. \tag{5}$$

Recent work on the viscous flow of liquids through soils (Carman, 1939) indicates that over a wide range of values of S the liquid moves as though its actual path through the soil made an angle of 45° with the direction of the maximum pressure gradient, i.e. l/l_e is approximately $1/\sqrt{2}$. As the diffusing gas molecules must follow the same paths we may anticipate the establishment of the following relation, for a certain range of S at least,

$$D = D_0 S/\sqrt{2}.$$

General treatment of diffusion measurements. For the steady state we have

$$\frac{dq}{dt} = \frac{D}{\beta} A \frac{p_1 - p_2}{l}.$$

The value of D depends upon the absolute temperature and the total pressure, the relation for most gases and vapours being

$$D_{T,P} = D \left(\frac{T}{273}\right)^2 \frac{P_0}{P},$$

where P_0 is 1 atm. The constant β is a function of temperature, since $1/\beta$ is the concentration in mg./c.c. at 1 mm. pressure, and we have

$$\beta = \beta_0 \frac{T}{273}.$$

Thus we have for the rate of flow in mg./sec.

$$\frac{dq}{dt} = DA \frac{p_1 - p_2}{l} \left(\frac{T}{273}\right)^2 \frac{P_0}{P} \beta_0 \left(\frac{T}{273}\right)$$

$$= \left(\frac{p_1 - p_2}{\beta_0} \frac{T}{273}\right) \left(D \frac{A}{l} \frac{P_0}{P}\right),$$

which we may write

$$C = E \times 1/Z$$

or current = diffusion potential difference ÷ impedance. As indicated above, C will be measured directly, E is a function of temperature only and a table of values can be drawn up for ready reference.

A typical value of E is obtained as follows. At 15° C. the vapour pressure of carbon disulphide is 242 mm. The value of β_0 is $\dfrac{760 \times 21{,}900}{76 \times 1000} = 219$, since 76 g. CS_2 vapour occupy 21,900 c.c. at 0° C. and 760 mm. pressure. Therefore

$$E_{15\cdot0} = \frac{242}{219} \times \frac{288}{273} = 1\cdot165.$$

When E and C are known, Z can be calculated and corrected to 1 atm. A and l are constants of the apparatus and hence D can be found.

Solution of non-steady state equation. As already indicated above, solutions of the general equation for various boundary conditions can be obtained from standard mathematical texts. The results of the standard method of treatment for the special conditions which will be considered in the experimental section below are therefore given without detailed working. Consider a cylinder, length l, area of cross-section A, closed at one end and filled to the top with a porous solid such as sand or a soil. Imagine a small amount of liquid injected at a depth h below the open surface such that it forms a thin sheet of negligible thickness across the cylinder. The vapour will diffuse upward and downward, and we assume that any vapour passing out of the open surface is immediately carried away so that there is no accumulation of vapour in the atmosphere just above the cylinder. The emission of vapour from the surface can be considered in three stages: (*a*) there is a period during which the rate of emission increases from zero as the vapour begins to diffuse from depth h to the surface, (*b*) there is a steady state which begins when a uniform pressure gradient has been set up between h and the surface, and this lasts until all the liquid has evaporated, and (*c*) there is a final "decay" state following on (*b*), the pore-space between h and l being full of vapour at the beginning with a uniform gradient between h and 0. Stage (*c*) ends when all the vapour has passed out of the system.

Stage a ("*growth*" *stage*). The equation to be satisfied is

$$\frac{\partial p}{\partial t} = \frac{D}{S} \frac{\partial^2 p}{\partial x^2} \quad \text{for } t > 0.$$

The boundary conditions are

(i) At $t = 0$, $p = 0$ for all values of x except $x = h$.

(ii) For all t, $p = p_0$ at $x = h$ ($p_0 =$ vapour pressure of liquid),

$p = 0$ at $x = 0$ (i.e. at surface),

$\dfrac{\partial p}{\partial x} = 0$ at $x = l$ (i.e. no flow across the bottom of the cylinder).

The solution is in two parts:

In the range $h > x > 0$

$$p = p_0 \frac{x}{h} + \frac{2p_0}{\pi} \sum_1^\infty (-1)^n \frac{1}{n} \exp\left[-\frac{n^2\pi^2}{h^2} \frac{D}{S} t \right] \sin \frac{n\pi x}{h}.$$

In the range $l > x > h$

$$p = p_0 - \frac{4p_0}{\pi} \sum_0^\infty \frac{1}{2n+1} \exp\left[-\left(\frac{2n+1}{l-h} \frac{\pi}{2}\right)^2 \frac{D}{S} t \right] \sin \frac{2n+1}{l-h} \frac{\pi}{2} (x-h),$$

a result which is only needed to provide analytical confirmation of the eventual uniformity of pressure ($p = p_0$ for all values of x) for large values of t.

The rate of emission from the open end depends upon the pressure gradient at $x = 0$. We have,

$$\frac{\partial p}{\partial x} = \frac{p_0}{h} + \frac{2p_0}{\pi} \sum_1^\infty (-1)^n \frac{1}{n} \exp\left[-\frac{n^2\pi^2}{h^2} \frac{D}{S} t \right] \frac{n\pi}{h} \cos \frac{n\pi x}{h}$$

and at $x = 0$ this becomes

$$\frac{\partial p}{\partial x} = \frac{p_0}{h} + \frac{2p_0}{h} \sum_1^\infty (-1)^n \exp\left[-\frac{n^2\pi^2}{h^2} \frac{D}{S} t \right].$$

From equation 3 we have, remembering that $\partial p/\partial x$ is positive in this case,

$$\frac{\partial q}{\partial t} = \frac{D}{\beta} A \frac{\partial p}{\partial x}$$

$$= \frac{D}{\beta} A \frac{p_0}{h} \left\{ 1 + 2\sum_1^\infty (-1)^n \exp\left[-\frac{n^2\pi^2 Dt}{h^2 S} \right] \right\}. \tag{6a}$$

As $t \to \infty$, this becomes

$$\frac{\partial q}{\partial t} = \frac{D}{\beta} A \frac{p_0}{h}, \tag{6b}$$

which is the equation for the steady state (b) in which the pressure gradient is uniform and equal to p_0/h. The series generally converges rapidly and in practice few terms are necessary even for small values of t.

Stage c ("decay" stage). With a new zero for time, i.e. measuring time from the instant at which the last part of the liquid vaporizes, we have the following conditions at $t = 0$. There is a uniform vapour pressure

(p_0) between $x=l$ and $x=h$ and a uniform pressure gradient (p_0/h) between $x=h$ and $x=0$. We have, as before,

$$\frac{\partial p}{\partial t} = \frac{D}{S}\frac{\partial^2 p}{\partial x^2} \quad \text{for } t>0.$$

Also,

$$\left.\begin{array}{ll} p=p_0 & \text{for} \quad l>x>h \\[2mm] p=p_0\dfrac{x}{h} & \text{for} \quad h>x>0 \end{array}\right\} \text{ at } t=0,$$

$$\frac{\partial p}{\partial x}=0 \quad \text{at } x=l \quad \text{for all } t,$$

$$p=0 \quad \text{at } x=0 \quad \text{for all } t,$$

and the solution is

$$p = \frac{8p_0 l}{h}\sum_0^\infty \frac{1}{(2n+1)^2\pi^2}\exp\left[-\left(\frac{2n+1}{2l}\pi\right)^2\frac{D}{S}t\right]\sin\frac{2n+1}{2l}\pi h \sin\frac{2n+1}{2l}\pi x,$$

$$\frac{\partial p}{\partial x} = \frac{8p_0 l}{h}\sum_0^\infty \frac{1}{(2n+1)\pi\cdot 2l}\exp\left[-\left(\frac{2n+1}{2l}\pi\right)^2\frac{D}{S}t\right]\sin\frac{2n+1}{2l}\pi h \cos\frac{2n+1}{2l}\pi x,$$

and at $x=0$

$$\frac{\partial p}{\partial x} = \frac{4p_0}{h}\sum_0^\infty \frac{1}{(2n+1)\pi}\exp\left[-\left(\frac{2n+1}{2l}\pi\right)^2\frac{Dt}{S}\right]\sin\frac{2n+1}{2l}\pi h,$$

and

$$\frac{\partial q}{\partial t} = \frac{D}{\beta}A\frac{p_0}{h}\frac{4}{\pi}\sum_0^\infty \frac{1}{2n+1}\exp\left[-\left(\frac{2n+1}{2l}\pi\right)^2\frac{Dt}{S}\right]\sin\frac{2n+1}{2l}\pi h. \quad (6c)$$

Two cases will be considered later.

(i) Put $h=l$, i.e. the diffusion takes place from the bottom of the cylinder. The values for the three stages become

(a)
$$\frac{\partial q}{\partial t} = \frac{D}{\beta}A\frac{p_0}{l}\left\{1+2\sum_1^\infty (-1)^n \exp\left[-\frac{n^2\pi^2 Dt}{l^2 S}\right]\right\}, \qquad (7\,i\,a)$$

(b)
$$\frac{\partial q}{\partial t} = \frac{D}{\beta}A\frac{p_0}{l}, \qquad (7\,i\,b)$$

(c)
$$\frac{\partial q}{\partial t} = \frac{D}{\beta}A\frac{p_0}{l}\left\{\frac{4}{\pi}\sum_0^\infty \frac{1}{2n+1}(-1)^n \exp\left[-\left(\frac{2n+1}{2l}\pi\right)^2\frac{Dt}{S}\right]\right\}. \qquad (7\,i\,c)$$

(ii) Put $h=l/2$, i.e. the diffusion takes place from a plane half-way down the cylinder:

(a)
$$\frac{\partial q}{\partial t} = \frac{D}{\beta}A\frac{2p_0}{l}\left\{1+2\sum_1^\infty (-1)^n \exp\left[-\frac{4\pi^2 n^2 Dt}{l^2 S}\right]\right\}, \qquad (7\,ii\,a)$$

(b) $\quad \dfrac{\partial q}{\partial t} = \dfrac{D}{\beta} A \dfrac{2p_0}{l},$ $\hspace{3cm}$ (7 ii b)

(c) $\quad \dfrac{\partial q}{\partial t} = \dfrac{D}{\beta} A \dfrac{2p_0}{l} \left\{ \dfrac{4}{\pi} \sum\limits_0^\infty \dfrac{1}{2n+1} \exp\left[-\left(\dfrac{2n+1}{2l}\pi\right)^2 \dfrac{Dt}{S} \right] \sin(2n+1)\dfrac{\pi}{4} \right\}.$

$\hspace{9cm}$ (7 ii c)

The presence of D/S in the exponential index of equations (a) and (c) shows that the rate of attainment of equilibrium depends upon this ratio, whilst the steady state rate depends upon D only (equation (b)).

The effects of solution and adsorption. When moisture is present in the soil it occupies part of the space which would otherwise be available for gas and vapour, and it will affect D by modifying the pore-space. There is a further effect if the diffusing material is soluble in water, as carbon dioxide and carbon disulphide are. Part of the material is removed from the vapour phase, and we may assume that the equilibrium between vapour and solution phases is instantaneously attained and that the concentration of the solution is proportional to the vapour pressure. Adsorption of the gas by the solid will also remove some of the material from the vapour phase, and if we may assume that the concentration in the condensed phases is proportional to the concentration in the vapour phase, we can treat both effects together. As in the few cases so far examined the amount adsorbed appears to be much greater than the amount dissolved, we use the term adsorption to cover both effects.

Consider the material present at a given part of a porous system as being divided between a vapour phase, exerting a pressure p, and an adsorbed phase in equilibrium with it. Let N mg./c.c. of system be the total concentration, and let n mg./c.c. of system be the vapour concentration. Then $p = \beta n/S$. We assume that $n/N - n$ is independent of N, i.e. n/N is constant, and $= \gamma$ say. The steady state will not be affected; once a uniform pressure gradient is set up our previous equation will hold:

$$\frac{\partial q}{\partial t} = -\frac{D}{\beta} A \frac{\partial p}{\partial x}. \hspace{2cm} (3)$$

For the non-steady state, the equation

$$\frac{\partial q}{\partial t} = \frac{D}{\beta} A \, \delta x \, \frac{\partial^2 p}{\partial x^2}$$

is modified by setting

$$q = A \, \delta x \, N = A \, \delta x \, \frac{n}{\gamma} = A \, \delta x \, \frac{pS}{\beta \gamma},$$

I.e.

$$\frac{\partial q}{\partial t} = \frac{A\,\delta x S}{\beta\gamma}\frac{\partial p}{\partial t},$$

or

$$\frac{\partial p}{\partial t} = \frac{\gamma D}{S}\frac{\partial^2 p}{\partial x^2}. \qquad (8)$$

The coefficient of pressure diffusion, previously D/S, thus becomes $\gamma D/S$, and as γ is less than unity the effect of adsorption is to reduce the rate at which pressure redistribution takes place, and the non-steady state rates of emission from the cylinder (i) (*a*) and (*c*), (ii) (*a*) and (*c*), given above, will be modified by the inclusion of a further factor γ in the exponential index. For example equation (7 i *c*) becomes

$$\frac{\partial q}{\partial t} = \frac{D}{\beta}\,A\,\frac{p_0}{l}\left\{\frac{4}{\pi}\sum_{0}^{\infty}\frac{1}{2n+1}\,(-1)^n\exp\left[-\left(\frac{2n+1}{2l}\,\pi\right)^2\frac{\gamma Dt}{S}\right]\right. \qquad (9\ \text{i}\ c)$$

and corresponding equations (9 i *a*), (9 ii *a*) and (9 ii *c*) can be written down.

EXPERIMENTAL

Apparatus. The cylindrical brass diffusion apparatus used for vapours is shown in section in Fig. 1. A collar, *C*, screws into a reservoir *R*, and resting in a groove in *C* is a stiff disk of copper gauze, *G*, on a rubber
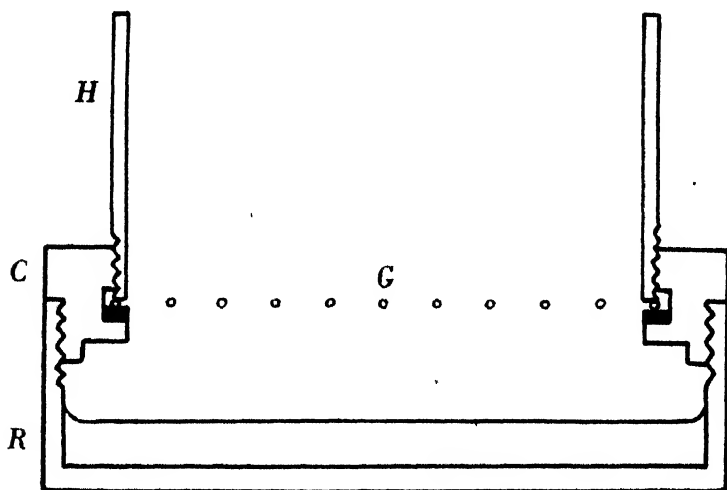

Fig. 1. Section of diffusion apparatus.

gasket. Screwed down hard on *G* is a short length of brass tubing, *H*, forming the soil holder. In practice, *C* and *H* form one unit—referred to below as the holder—and the reservoir a second unit. The original intention was to have *G* replaceable so that different size meshes could

be used, but as fine gauze cannot be kept flat, especially with a load on it, a permanent stiff grid is now maintained at G, and this is used as a support for finer gauzes necessary to prevent the solids from slipping through the grid. The dimensions are

H depth = 2·64 cm.; area = 22·3 sq. cm.

R depth = 1·6 cm.;   area = 34 sq. cm.

Total weight, empty = 235 g.

Total weight, full, varies from 248 to 360 g.

Preliminary experiments with carbon disulphide showed that a suitable balance should weigh to 10 mg. and be capable of taking loads up to 400 g. The balance employed is an Avery balance, weighing up to 500 g., fitted with a pointer and scale reading from 0·00 to 1·00 g. and graduated in $\frac{1}{100}$ g. The fitting of a lens enables readings to half a division to be made, i.e. to 5 mg.

The method of experiment is to pour a known volume of liquid into R, screw in the soil holder and contents, counterpoise on the balance and then determine the rate of loss of weight by reading the pointer at intervals. The balance is in a large case with doors at the back and front, and by keeping both slightly open there is sufficient ventilation to ensure that the vapour pressure above the soil never reaches a value large enough to invalidate the assumption that it is maintained at zero. Too violent a through draught sets the balance pans swaying, and errors arise from the consequent disturbance of the liquid level in the reservoir. A thermometer hangs in the balance case and the temperature is recorded as part of every observation. Readings are usually taken every 20 min., and an experiment lasts about 360 min. The method of determining D from the results will be illustrated later after the reservoir correction has been considered.

Liquids used. Carbon disulphide has been the principal material used, as its vapour pressure at ordinary temperatures is sufficient to produce measurable rates of evaporation even through solids of very low porosity, but not so great as to have large temperature variations. It has the further advantage that it is a commercial soil fumigant. Acetone is not quite so good as an experimental liquid, and fewer results have been obtained with it.

Porous solids. A wide range of granular solids has been used so that all sorts of shapes and sizes of pores might be available. A wide range of pore-space values has been covered, and sufficient soil experiments have been included to show that soils conform to the general behaviour.

Values of D_0 for carbon disulphide and acetone. The values quoted in the literature for the coefficient of diffusion of carbon disulphide into air vary from 0·088 (*I.C.T.*) to 0·0995 (Mellor, 1925*a*). As the value of D_0 is required in later calculations a redetermination was made. The rate of evaporation of carbon disulphide from the bottom of a cylindrical jar was measured, and, assuming a uniform partial pressure gradient when the steady state was attained, an estimate of D_0 was made. The mean of five determinations gave $D_0 = 0·103$ cm.²/sec.

This value is a few per cent higher than any previously recorded, and the difference can be accounted for by our use of an approximation. The basic theory outlined in the preceding pages only holds for two gases interdiffusing because of small partial pressure gradients; the experiments were concerned with one-way motion of a vapour through a stationary gas (air), and the partial pressure gradients were large. The effect of the latter is to introduce an error of 1 or 2 % due to the variation of the coefficient of diffusion with the relative proportions of the vapour-air mixture, whilst the effect of the one-way motion is to produce a non-linear partial pressure gradient in the steady state, leading to a further error, in the same sense, of a few per cent. The value of D_0 is, therefore, some 5–10 % larger than the true coefficient of diffusion of carbon disulphide vapour into air, but as the nature of the correction will be the same for all the determinations of D reported below, the ratio D/D_0 will be free from significant error. There will, of course, be an uncertainty of 2 or 3 % in the values of the ratio, but we shall see that this is less than the scatter of the experimental results for porosities of technical interest, and the order of accuracy obtained will be quite adequate for the present purpose. Until there is a need for more precise measurements, one may reasonably ignore second-order corrections, whether arising from this approximation to the basic theory, the uncertainties of which have been outlined by Chapman (1928), or from the criticisms of the evaporation method of measuring diffusion coefficients which have been made by Trautz & Müller (1935). In a separate account a more exhaustive discussion of the physical aspects of the problem will be provided; further elaboration is unnecessary here.

Similar determinations were made for acetone, the mean of two giving $D_0 = 0·095$ cm.²/sec. There does not appear to be any record of a previous determination of the coefficient of diffusion of acetone vapour into air.

Reservoir correction. As will be seen from Fig. 1, the vapour-pressure drop between the surface of the liquid and the surface of the soil is not

effectively applied to the faces of the soil. There is a drop between the liquid surface and the bottom of the soil sample, and a further drop across the sample, and it is this latter which we need for calculations of diffusion rates. The necessary reservoir correction is obtained as follows.

Let Z_0 be the impedance of the reservoir and gauze together and let Z be the impedance of the material in the holder. The total impedance is thus $Z_0 + Z$, and if the diffusion potential difference is E, the observed diffusion current, C, will be given by $Z + Z_0 = E/C$. If now an experiment be performed with air in the holder, we have $Z = l/D_0 A$, and hence Z_0 can be calculated. The value of Z_0 is found to be practically independent of the amount of liquid in the reservoir, indicating that the main part of it is due to the impedance of the gauze. The values of Z_0 obtained with (a) a disk of 200-mesh copper gauze on G, (b) a disk of silk fabric on G, are

(a) $Z_0 = 0.76$, (b) $Z_0 = 0.78$ for CS_2. (b) $Z_0 = 0.88$ for acetone.

Steady state determination of variation of D with S. The routine followed is to pack the granular solid into the holder, without undue pressure so that G is not strained. The holder and sample are weighed, and the weight of the holder and density of the solid being known, the volume of the solid is found. This is expressed as a fraction of the volume of the cylinder H. The liquid is poured into the reservoir, the two parts screwed together, and a rubber band slipped over the line of contact of the two parts to ensure that there is no leakage from the reservoir. Observations of time, weight and temperature are made at half-hour intervals and the mean diffusion current (c) found. The calculation then proceeds as follows.

Rothamsted subsoil (air-dry) on fabric; 8 c.c. CS_2. Barometer 29·30 in.

Weight of soil + holder = 222·25 g.

Weight of holder $\quad = 151\cdot47$ g.

Weight of soil $\quad = \overline{\quad 70\cdot78}$ g.

Volume of soil $\quad = \dfrac{70\cdot78}{2\cdot50} = 28\cdot3$ c.c.

Volume of holder = 58·8 c.c. $\therefore S = 0\cdot518$.

Experiment lasted 360 min. Readings during the first 80 min. were ignored.

$$\bar{C} = 2\cdot260 \times 10^{-1} \text{ mg./sec.} \quad \bar{\theta} = 12\cdot7^\circ \text{ C.}$$

$$E_{12\cdot7} = 1\cdot058$$

$$\therefore Z + Z_0 = 4\cdot54 \qquad\qquad l = 2\cdot64 \text{ cm.}$$

$$(Z + Z_0)_{30} = 4\cdot64 \qquad\qquad A = 22\cdot30 \text{ cm.}^2$$

$$Z = 3\cdot86.$$

$$\therefore D = \frac{2\cdot64}{22\cdot30} \times \frac{1}{3\cdot86} = 0\cdot0307 = 0\cdot103 \times 0\cdot298.$$

A complete list of results obtained in this way appears in Table I, and a graphical representation in Fig. 2. The results for carbon disulphide and acetone through air-dry solids, and for carbon disulphide through moist soils are all included in Fig. 2 by taking D/D_0 as ordinate. The steady state results for moist soils involve a correction for the moisture which evaporates during an experiment, and it is assumed that the water-vapour loss proceeds at a uniform rate. An estimate of its amount is obtained by weighing soil and holder when all the carbon disulphide has passed out, i.e. when the rate of loss becomes constant again, and comparing with the corresponding reading taken at the beginning of the experiment. The order of magnitude of the correction will be seen

Table I

(a) *Diffusion of carbon disulphide vapour*

(i) Air-dry solids

Material	S	Mean temperature ° C.	D/D_0
Sand	0·357	16·6	0·249
	0·372	15·4	0·245
	0·374	15·4	0·248
	0·378	15·5	0·252
	0·381	15·6	0·252
Sand mixture	0·155	13·0	0·109
	0·164	15·6	0·124
	0·205	14·0	0·120
	0·232	15·0	0·145
	0·267	14·4	0·176
	0·275	10·8	0·168
	0·300	16·4	0·206
Common salt	0·452	14·4	0·279
	0·475	18·5	0·294
	0·545	14·4	0·350
	0·610	17·5	0·420
Talc	0·705	17·2	0·536
	0·742	14·0	0·548
	0·756	15·3	0·590
Kaolin	0·772	16·0	0·598
	0·782	17·6	0·600
Kieselguhr	0·844	15·6	0·677
	0·924	15·0	0·805
Steel wool	0·93	16·9	0·815
Glass spheres:			
Large, $d = 3$ mm.	0·397	16·7	0·319
Small, $d \doteqdot \frac{1}{2}$ mm.	0·364	17·0	0·282
Mixture	0·185	15·5	0·151
Mica	0·85	14·2	0·494
	0·88	18·8	0·304
	0·89	18·2	0·380

Table I (continued)

(ii) Soils

Material	Moisture content %	S	Mean temperature °C.	D/D_0
Rothamsted subsoil	Air-dry	0·518	12·7	0·298
	,,	0·518	13·8	0·304
	,,	0·547	14·3	0·346
	,,	0·550	16·5	0·358
	11·0	0·438	18·4	0·278
	17·0	0·448	16·7	0·297
	25·0	0·626	17·2	0·442
	29·6	0·549	16·8	0·364
Rothamsted subsoil + sand	Air-dry	0·422	15·1	0·273
Natal soil (N 64)	,,	0·496	16·8	0·300
	,,	0·620	16·4	0·417
	,,	0·676	17·1	0·475
	11·0	0·475	17·0	0·312
	19·3	0·355	19·4	0·249
	22·0	0·425	14·9	0·299
	30·6	0·195	17·0	0·118

(b) Diffusion of acetone vapour

Material	S	Mean temperature °C.	D/D_0
Mixture	0·155	14·4	0·105
Sand	0·355	17·0	0·244
Rothamsted subsoil	0·537	16·3	0·307
N 64	0·622	16·2	0·410
Kaolin	0·772	14·7	0·566
Kieselguhr	0·844	14·4	0·677
,,	0·924	13·7	0·792

from some data given below (p. 455) or from Fig. 3, where the "mean zero line" represents the steady water loss.

Six points have been specially marked on Fig. 2. Three represent results for diffusion through systems of glass spheres (△); in descending order of D/D_0, large, small, and a mixture of large and small spheres. The other three points (□) represent results for mica with different types of packing. The largest value of D/D_0 was obtained when the holder was packed with its cylindrical axis horizontal. For reasons detailed below these six points have been ignored in drawing the curve.

DISCUSSION OF RESULTS FOR STEADY STATE

With the exceptions noted, the experimental points lie on or near a curve which passes through the origin. Before discussion the implications of this curve, some consideration must be given to possible sources of experimental error.

Temperature changes. Variations in temperature in the course of an experiment will cause expansion or contraction of the air-vapour mixture, thus disturbing the assumed steady state. In practice the total change was rarely more than 1° C., and being spread over several hours the possible effects can be neglected.
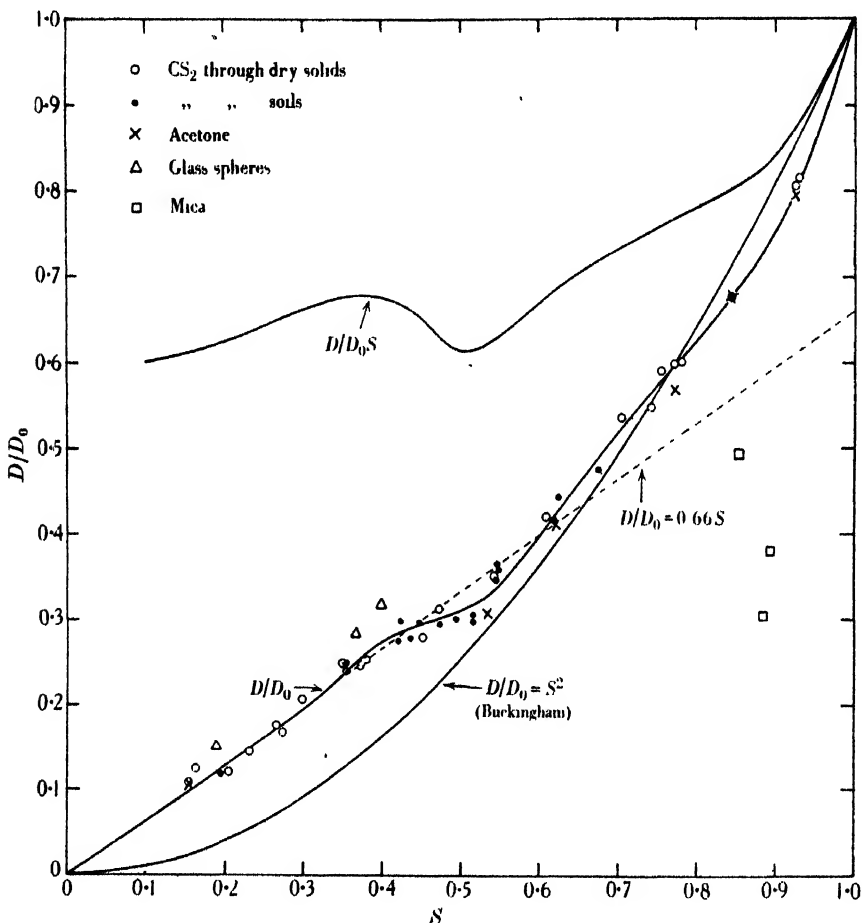
Fig. 2. Dependence of coefficient of diffusion on porosity.

Measurement of time and weight. These are two measurements which can usually be taken as absolute. The balance scale was periodically recalibrated, and as in the aggregate a determination of D depends on the measurement of a change in weight of several grammes, the readings are probably correct to 1 part in 500.

Measurement of pore-space. This depends on correct determinations of the density of the solid and of the volume of the holder. The latter

is a constant of the experiments, and any error in its determination will cause a displacement of all points but will not affect the scatter of the points. The sensitivity of S to errors in the density determinations varies, being given as $\delta S = (1-S)\,\delta\rho/\rho$. Thus, assuming an error of 1 % in ρ, the errors in S will be: 0·001 at $S=0·90$, 0·005 at $S=0·50$, and 0·009 at $S=0·10$. Most of the density measurements were more accurate than this, particularly between $S=0·1$ and $S=0·4$, where the materials employed were chiefly sands or mixtures of sands.

Packing "errors". The theoretical discussion above (p. 440) is based on the assumption that the solids are randomly packed and that there is no marked anisotropy in any of the systems. This is an ideal state of affairs and in practice we cannot expect anything better than a good approximation to this ideal state. There are three sources of packing errors: (*a*) With large particles in the holder, edge effects are to be anticipated, because there will be comparatively straight paths available for vapour molecules to pass along the walls of the holder. This leads to an over-estimate of the coefficient of diffusion, and as this condition is considered to have arisen in the experiment with large glass spheres, the corresponding point on the graph has not been given any weight in drawing the curve. (*b*) Small particles may fill the meshes of the supporting gauze and thus increase the impedance of the lower system. Errors arising in this way cannot be entirely eliminated, but they have been cut down as far as possible by choosing the more suitable of the two supports employed, i.e. either the 200-mesh gauze or the silk fabric, according to the particle size of the experimental material. (*c*) The formation of air pockets and culs-de-sac in packing, particularly with mixed sizes of particles, will affect diffusion rates, and it is thought that this is the major cause of the scatter of the experimental points. The marked effect of anisotropy of structure is shown very clearly in the results for mica, and it is obvious that general conclusions from the data will not apply to this or any other laminated solid.

Atmospheric changes. Throughout this discussion it has been assumed that the air into which diffusion takes place is of fixed composition. This is not so, and a small part of the scatter can reasonably be attributed to variations in relative humidity.

Both of these last-mentioned sources of scatter will be present in field experiments, and we may therefore accept the mean curve as showing how an ideal field soil would affect diffusion of gases and vapours through it.

The experimental results plotted in Fig. 2 show several points of

interest. In the first place, the curve drawn is adequate for both carbon disulphide and acetone vapours, a result anticipated in the preliminary survey. Comparing the curve with the parabolic curve obtained by Buckingham for carbon dioxide, we find a marked divergence for values of S below 0·7, and this divergence is greatest in the region of practical importance, namely for values of S below 0·50. *A priori* one would expect carbon dioxide to show the same behaviour as the vapours, and a probable explanation of the conflicting experimental evidence will be given in discussing the effects of adsorption. For the moment, we accept the new curve as universally true, and note that diffusion is even less affected by the solid than Buckingham found it to be. The scatter of the experimental points introduces some uncertainty into the drawing of the best curve, and it is possible that the decrease in slope between $S = 0·40$ and $S = 0·55$ is not as pronounced as the curve suggests. The decrease is shown more strikingly in the plotting of $D/D_0 S$ against S. (This has been plotted from the curve and not from the experimental points.) The derived function represents the ratio l/l_e (equation (5)) which will be dependent on the pore-geometry of the solid, but before any conclusions about the nature of the packing can be safely drawn, more detailed investigation in this porosity range will be necessary. At small porosities the derived curve is too sensitive to variations in D/D_0 to permit a useful direct comparison with Carman's results for liquid flow, and a more effective comparison can be made from the mean straight line (dotted) which has been drawn to show the dependence of D/D_0 on S in the range $0·0 < S < 0·6$, a range which covers the porosities of technical interest. The slope of this line is 0·66 and this is a measure of the ratio of the actual length of the soil column to the effective length. Carman's value, which his experimental results indicate as probably being too big, is $1/\sqrt{2}$, i.e. 0·707. The agreement is good and provides support of the assumption that diffusion through a porous body is primarily a function of the geometry of the body and is independent of the nature of the diffusing material. The effective path lengths are determined by the distances the vapour molecules must travel to pass around the solid particles, and one would expect them to be slightly shorter for spherical particles than for particles of less regular shape. The coefficient of diffusion should therefore be slightly greater through a system of spheres than through any other system of particles, and this is experimentally confirmed by the recorded values. The corresponding points lie above the curve, the departure being greatest for the large spheres, but, as we have seen, part of this can be ascribed to an edge

effect. As the primary object of this work is to obtain a curve which can be applied to soils, the results for spheres have not been considered in drawing the curve.

THE EFFECTS OF SOLUTION AND ADSORPTION

A few non-steady state experiments have been carried out with moist soils using carbon disulphide as the diffusing vapour. From the published data on the solubility of carbon disulphide in water (Mellor, 1925b) it is possible to make an estimate of γ (see p. 445) assuming that there is no adsorption taking place, and a theoretical "decay" curve can be drawn. The experimental curves were found to have a slower rate of decay, indicating that γ was much less than the estimate based on the solvent action of the soil moisture. The disagreement was attributed to the occurrence of adsorption and this was confirmed by weighing the soil and holder during the steady state. After making allowance for the water loss, marked increases in weight were found; these were presumably due to the adsorbed carbon disulphide. Knowing the pore-space, it was possible to calculate the weight of vapour present in the soil and thus to obtain an effective value of γ.

The design of the apparatus does not conform to that assumed in the theoretical analysis of p. 442, because of the reservoir below the soil. This is not allowed for in calculating γ, which will be somewhat under-estimated. At the same time the content of the soil during the steady state has been estimated by assuming that the whole of the vapour pressure difference is exerted across the soil, leading to an over-estimate of γ. The two effects thus tend to annul each other and we may expect some sort of agreement between theory and practice if we assume that our diffusion apparatus does behave like an ideal cylinder: exact agreement will be fortuitous. Reasonable agreement has been found and a typical experiment will be quoted in detail.

Moist Rothamsted subsoil: Moisture content $= 17 \cdot 0 \%$.

Barometer reading 29·80 in.

Weight of soil + holder ($t = 0$ min.) $= 223 \cdot 81$
($t = 262$ min.) $= 223 \cdot 73$
($t = 500$ min.) $= 222 \cdot 86$.

Net loss of water in 500 min. $= 0 \cdot 95$ g.
Net loss of water in 262 min. $= 0 \cdot 50$ g.
Actual loss in weight in 262 min. $= 0 \cdot 08$ g.
$\therefore$ net gain in CS_2 $= 0 \cdot 42$ g.

Volume of vapour $= 58\cdot8 \times S = 26\cdot3$ c.c. $(S = 0\cdot448)$.

Mean pressure of vapour $= \frac{1}{2} \times 261 = 130$ mm. (at $17°$ C.).

β at $17°$ C. $= 219 \times \dfrac{290}{273} = 232$.

$\therefore$ weight of vapour $= \dfrac{26\cdot3}{232} \times \dfrac{130}{760} \times 76 \times 10^3$ mg.

           $= 14\cdot7$ mg.

Total content of soil at 262 min. $= 420$ mg.

$$\therefore \gamma = \frac{14\cdot7}{420} = 0\cdot035.$$

Considering the decay state only, the theoretical expression (p. 446) is

$$\frac{\partial q}{\partial t} = \frac{D}{\beta} A \frac{p_0}{l} \left\{ \frac{4}{\pi} \sum_0^\infty \frac{1}{2n+1} (-1)^n \exp\left[-\left(\frac{2n+1}{2l}\pi\right)^2 \frac{\gamma D t}{S} \right] \right\}, \quad (9 \, i \, c)$$

in which the first group of terms represents the steady state rate of emission. The exponential index contains a factor $D/l^2 S$ to which some correction for the reservoir must be applied. We have $Z = l/DA$ and if V is the volume of the system $(= lA)$, $Z = l^2/DV$, i.e. $D/l^2 = 1/VZ$. It is proposed, as a first approximation, that instead of $D/l^2 S$ the value of $1/\Sigma VZS$ be used in the exponential index. In this particular case

for H we have $V = 58\cdot8$, $S = 0\cdot448$, $Z = 4\cdot11$, $VZS = 108$,

for R we have $V = 41\cdot0$, $S = 1\cdot00$, $Z = 0\cdot76$, $VZS = 31$.

The value of $1/\Sigma VZS$ obtained from these quantities will be that for $0°$ C. and 30 in., and to obtain the values for the conditions of the experiment the temperature and pressure corrections must be applied: we obtain

$$\frac{D}{l^2 S} = 0\cdot0082, \quad \therefore \frac{\pi^2 \gamma D}{4 l^2 S} = 7\cdot05 \times 10^{-4}.$$

The equation of the decay state may thus be written as

$$C = C_0 \frac{4}{\pi} \Sigma \frac{1}{2n+1} (-1)^n \exp\left[-(2n+1)^2 \, 7\cdot05 \times 10^{-4} t \right].$$

After about 20 min. $(t = 1200)$ only one term in the series is necessary, and the equation reduces to the simple form of

$$C = C_0 \frac{4}{\pi} \exp\left[-7\cdot05 \times 10^{-4} t \right].$$

The experimental points and theoretical curve are shown in Fig. 3. This rapid convergence of the series makes a comparison of theoretical and experimental curves somewhat simpler. If the experimental points are plotted logarithmically the decay curve becomes a straight line from the

slope of which γ can be calculated and compared with the value obtained by direct weighing of the soil and holder during the steady state. The results of two experiments on Natal soil have been treated in this way and the agreement is very good.
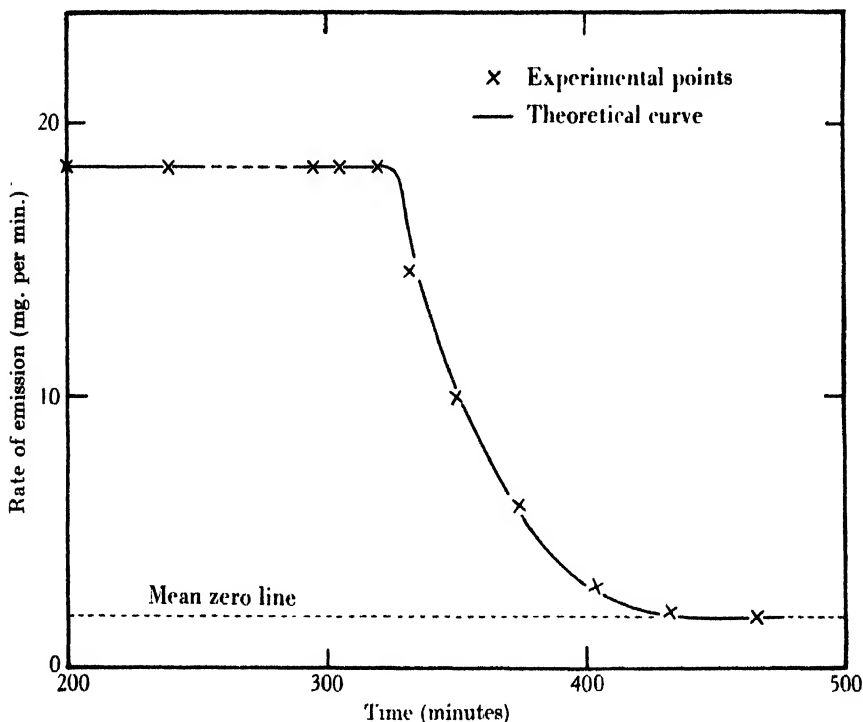

Fig. 3. Rate of emission of carbon disulphide vapour from moist Rothamsted soil.

Table II

Soil	Moisture %	S	γ (from weighing)	γ (from slope)
Natal 64	19·3	0·355	0·025	0·026
	22·0	0·425	0·026	0·024

As the theoretical basis of these experiments on adsorption has yet to be established and the apparatus used does not conform to the ideal laid down in the theoretical analysis, no useful purpose will be served by extending the above table. Taken in conjunction with Fig. 3 it demonstrates the adequacy of the technique employed in handling adsorption data, suggests that the basic assumptions are probably reliable, and indicates that with better choice of experimental conditions the theoretical prediction of the effect of adsorption will be realized in practice.

factor, the pore-space, and the temperature, the spreading of carbon disulphide vapour through soil can be quantitatively described. The principal assumption made, namely that γ is constant at all vapour pressures, is one which requires further experimental confirmation. The constant will vary with the moisture content of the soil and probably from soil to soil. In addition to γ being constant, the theory requires that the equilibrium between the two phases should be instantaneously attained. This may not be so and there may be a lag between the pressure changes and the attainment of equilibrium. Such a time lag would account for the phase difference between the observed and theoretical curves of Figs. 4 and 5. The amount is not very great and is probably
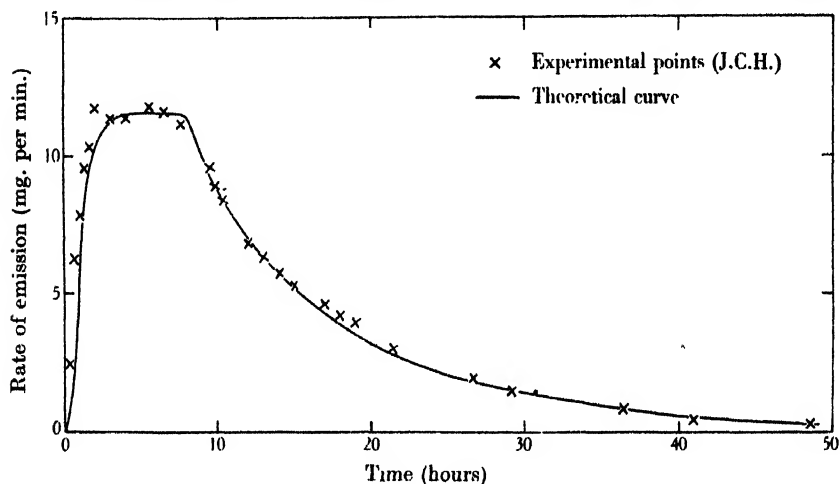

Fig. 5. Rate of emission of carbon disulphide vapour from surface of cylinder of soil 12 in. deep. Injection: 6 in. deep.

less than the differences which will be found in field soils arising from chemical and biological action, physical heterogeneity and temperature variations.

Examination of these adsorption results brings out one point which has an important bearing on the steady-rate experiments. For a soil sample little more than 1 in. thick the time taken to set up the steady state varies from 40 to 100 min., depending on the type of soil, pore-space and moisture content. In the case of the 6 in. columns of New Zealand soil the time is about 3 hr. and would probably be greater for smaller pore-space. It is obvious that reliable steady state measurements can only be made when this growth stage is ended: hence the neglect of the readings during the first 80 min. of the experiment quoted on p. 449. One can reasonably expect that carbon dioxide will behave in the same

way although the times may be different. In Buckingham's experiments a 4 in. column of soil was used and readings were taken after an interval of 20–30 min. It is highly probable that in no case had the steady state been attained when the observations were made and, as a consequence, that all values of the diffusion coefficient were under-estimated, the error being greatest for the smallest values of the porosity. Thus we have a qualitative explanation for the difference between the present steady state results and the results of Buckingham. As carbon dioxide is the gas about which information is most desired, some direct diffusion measurements will be made and the suggested explanation of the discrepancy tested quantitatively.

Summary

The dependence of the coefficient of diffusion, D, upon the porosity, S, of a granular solid is investigated experimentally. For steady state conditions, using carbon disulphide and acetone vapours, it is shown that a curve connecting D/D_0 and S can be drawn which is independent of the nature of the solid, its moisture content and, within limits, its texture. For a limited range of values of S ($0.0 < S < 0.7$) a good approximation is $D/D_0 = 0.66S$ and over this range the diffusion coefficients are larger than those found by Buckingham for carbon dioxide.

Investigation of the non-steady state shows that in soils the attainment of pressure equilibrium is retarded by adsorption, and it is suggested that Buckingham's low values for steady-state conditions can be attributed to premature observations of the diffusion rates; the steady state had probably not been attained when his measurements were made.

References

Buckingham, G. (1904). *Bull. U.S. Dep. Agric.* no. 25.
Carman, P. C. (1939). *J. agric. Sci.* **29**, 262.
Chapman, S. (1928). *Phil. Mag.* **5**, 630.
Higgins, J. C. & Pollard, A. G. (1937). *Ann. appl. Biol.* **24**, 895.
I.C.T. (*International Critical Tables*) (1929). **5**, 62. New York.

KEEN, B. A. (1931). *The Physical Properties of the Soil*, chap. 10. London.

MELLOR, J. W. (1925a). *Comparative Treatise on Inorganic and Physical Chemistry*, **6**, 99. London.

—— (1925b). *Comparative Treatise on Inorganic and Physical Chemistry*, **6**, 109. London.

ROMELL, L.-G. (1922). *Medd. Stat. Skogsforsoks.* **19**, 125.

SMITH, F. B. & BROWN, P. E. (1933). *Soil. Sci.* **35**, 413.

TRAUTZ, M. & MÜLLER, W. (1935). *Ann. Phys., Lpz.*, **22**, 313.

STUDIES ON THE METABOLISM OF FOWLS

III. THE DETERMINATION OF THE COMPARATIVE NETT ENERGY OF SUSSEX GROUND OATS AND WHITE MAIZE MEAL FOR FATTENING COCKERELS

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(With Two Text-figures)

INTRODUCTION

THERE are two fairly well-defined methods for measuring the thermic energy of a feeding-stuff. In the first, the animal is maintained at a steady level of metabolism either by starving it or by feeding it for a period at a maintenance level, and a single feed of the ration to be investigated is then given. The total extra heat produced above the steady level is measured and taken as the thermic energy. Alternatively, in the second method, the feeding-stuff under investigation is fed steadily over a definite period in addition to the basal ration, if any, and the rise in heat production per day over the basal period is determined.

The older work on Specific Dynamic Action is mostly based on the first method, and it has been used more recently by Hamilton (1939). For the comparison of rations for feeding purposes there are three objections to the first method. First, the experiments of the present writers described in paper II of this series confirm the observations of Barott (1938) and other workers, that there is a diurnal rhythm of metabolism causing a variation in its level at different times of day, and that there is therefore no steady level of metabolism in fowls to which the observations may be referred. In the second place, for application to feeding practice it is necessary to find the effect when the ration is being fed to an animal over a period, which should, strictly speaking, be comparable in length with that for which it is proposed to feed the ration in practice. In some experiments by the first method these conditions are fulfilled by measuring the heat produced by a single feed following a period of starvation after the animal has been fed for a considerable time beforehand on the experimental ration (Hamilton,

1939). In this connexion it is permissible to refer to the recently published work of Møllgaard & Thorbek (1938), who find that the acid in A.I.V. silage, if not neutralized, has a powerful depressant effect on the NK_f value of this silage for cows, most probably due to cumulative acidosis. This effect would presumably not appear if a single feed only of the silage were given. A third objection to the method is that the value for the nett energy obtained cannot be related to any particular plane of nutrition. In view of what has been said we have adopted the second and more usual method in this work. It may be added that the possibility of a variation in the nett energy value with *time* envisaged in the experiments mentioned may possibly be concerned in the cases where nett energy varies as between animals of the same species, which have led one of the authors (T. D.) to conclude that it is an average value of a variable rather than a constant.

The object of the experiments described in this paper was to gain information as to whether the nett energy value of cereals for fowls depended only on their content of digestible or metabolizable nutrients, or if definite differences exist in the quantity of thermic energy produced by equal quantities of metabolizable energy from different cereals. In this country it is generally believed by practical feeders that Sussex ground oats has a nett energy value superior to that of maize and the other cereals, although digestibility experiments (Halnan, 1928 a, b) show that, of the two, maize is the more digestible. Maize has always been considered the "black sheep" of feeding-stuffs, although it has not been shown that its inadequacy is due to any positive factor present in it, but rather to its deficiencies. It seemed therefore that if there were in fact differences between the nett energy values of cereals, the comparison of Sussex ground oats with white maize meal, the reputed best and worst cereals, would be the most likely to show this clearly.

Most authorities, both in Europe and America, agree that the nett energy value of a feeding-stuff depends upon the balance of the ration in which it is incorporated, reaching a maximum value when this balance is optimal for the needs of the animal; and we set out to determine the nett energy under these optimal conditions, which correspond to those under which feeding should take place in practice. In "difference experiments", such as those reported in the present paper, the conditions of balance must of course apply to both the basal ration and the super-maintenance ration.

TECHNIQUE

Careful consideration has been given to the amount of repetition necessary owing to the considerable amount of labour involved in this type of work. The amount of labour depends rather on the amount of repetition than on the refinement of the individual experiments. Our problem therefore has been to design an experiment of sufficient refinement to give the desired precision with a minimal amount of repetition. In this connexion we do not feel that experiments on one or two animals, valuable though they may be when carefully carried out, are really a safe basis on which to found theories for general application. There may be individual differences in the physiological behaviour of different animals, and enough experiments must be carried out to get some idea of these differences, before any estimate of the precision of the average of the results can be made.

The following considerations have guided us in this matter. Thermic energy being, presumably, a small quota in cereals, compared with the nett energy, it appeared desirable that as much as possible of the supplement should be added to the basal ration in the supermaintenance periods, and that these should be as long as possible within the limits imposed by the ability of the bird to consume the feed steadily throughout the period. Actually, an amount of metabolizable energy between 1·7 and 2·6 times the maintenance heat production was fed to the different birds according to their appetites. The supermaintenance periods extended to 12 days—4 days preliminary and 8 days experimental period. In a few cases the supermaintenance periods were of shorter duration owing to failure of the appetites of the birds, but the experimental period was never less than 6 days. During maintenance feeding, the experimental period was extended to 10 days both to give a better average composition in the excreta and to relieve pressure on the staff. The total period of supermaintenance feeding thus corresponds closely to the normal period of 14 days trough feeding in fattening practice.

Corrections for weight changes are usual in this kind of experiment, but are unsatisfactory, since there is no agreement as to the precise correction which should be applied even in fasting ruminants—not to mention fowls, on which much less work has been done —while the divergence of view in this matter, where the difference between the same animal in fat and lean condition is in question, is very great. Furthermore, body weight is very variable from day to day, being dependent on changes of intestinal fill, and the weight correction, as usually applied,

would correspond to a large fraction of the thermic energy, of the order of 25% in these experiments on cockerels. We have therefore arranged our experiments so that the mean live weight during maintenance periods shall be as nearly as possible equal to the mean live weight in the supermaintenance periods and have made no weight correction.

We have attempted to exclude, to some extent, the possible variations in the nett energy values as measured on different birds. These variations may be divided into two parts, those caused by differences in the absolute nett energy values given by different birds on the same cereal, and those caused by differences in the relative reaction of different birds to the two cereals. We have excluded the first of these variations by the same method which Mitchell & Carman adopted in Mitchell's classical method for the determination of the biological values of proteins for growth and maintenance by the nitrogen balance method (Mitchell & Carman, 1924). That is, we have fattened the same bird twice, once on each super-maintenance ration. The second possible variation remains as part of the error of the experiment.

In the calorimeter tests we put the bird into the calorimeter as described below for periods of 3 hr. at different times of the day and night on several days. By this means we eliminated to a considerable extent any effect of possible day-to-day fluctuations of metabolism not involved in the normal diurnal rhythm. In addition, to get a reliable estimate of the metabolism from the 15 hr. total calorimeter time during the feeding period, we have controlled the activity by passing skewers over the bird's back when it is sitting down on the perch in the calorimeter to prevent it rising; thus there are no periods of standing which would have to be excluded from the results.

Forbes *et al.* (1935) deduced indirectly from their experiments on the effect of an inadequate supply of proteins on the thermic energy, that the extra heat production caused by the lack of balance of a ration low in protein could only be accounted for as increased activity. Hamilton (1939) could not confirm this by direct experiments. It did not appear that in our experiments any appreciable fraction of the thermic energy appeared as increased activity. We have found that the most important activity factor increasing the metabolism is the length of time spent standing (Deighton & Hutchinson, 1940). We therefore investigated the amount of time spent standing throughout the feeding periods from the records of the photoelectric apparatus (Deighton, 1939) to discover whether the ration influenced this, and activity observations were also made during the calorimeter tests as described later.

The experimental scheme was as follows: Two birds were used for experiment during the same experimental period of 8 or 10 days as the case might be, during which time each was tested in the calorimeter for 3 hr. in the morning, afternoon, evening, late at night, and at dawn (about 4 or 5 o'clock in the morning). This was done with the two birds, first on a maintenance ration, then on one of the supermaintenance feeds, after which a weight-adjustment period was intercalated in which no tests were performed, and the bird was fed at a submaintenance level, until it was calculated that the fat deposited in the supermaintenance period had been lost. This was followed by further similar experiments on the other supermaintenance ration, and finally a second set at maintenance level. Bird N broke its beak during the experiment and had to be replaced by bird O. Later it went through the remaining periods after it had recovered.

Benedict & Lee (1937) consider that in differential direct calorimetric measurements of this nature it is important to take into account the effect of changes of body temperature on the heat emission of birds during the periods in the calorimeter. They found that the rectal temperature of geese fell about 1° C. during confinement for 6 hr. in their calorimeter, whether the geese were in the post-absorptive state or had been previously stuffed. However, with cocks and hens Benedict et al. (1932) found a fall of only 0·2–0·3° C. in the post-absorptive state and were uncertain whether the fall was due to "the small amount of struggle on the part of the bird" consequent on preparing it and placing it in the chamber. It appears therefore that this factor has a relatively unimportant effect on direct calorimetric measurements with fowls, especially when as in our experiments there is a preliminary period of ½ hr. after the bird is placed in the chamber before measurements of the heat emission are made. In any case such an effect could only influence the absolute nett energy measurements, and not the comparative values of the two cereals.

The birds were kept in the laboratory for some weeks before the commencement of the tests, as it is known that the energy metabolism of animals in general tends to fall for a time when they are subjected to confined conditions.

The fowls used were all adult Light Sussex cockerels 9–12 months old, and were kept closely confined in cages at an equable temperature around 20° C., that is, under conditions not greatly differing from fattening practice. Each bird was given several practice runs in the calorimeter to accustom it to the technique before the experiments began.

All the birds were given the same basal ration, which was fed at 8.0 a.m. and 5.0 p.m. (9.0 a.m. and 6.0 p.m. during the period of "summer time"). The daily supermaintenance rations consisted of the same quantity of this basal ration as was fed in the maintenance period to which a supplement of Sussex ground oats or white maize meal was added.

The basal or maintenance ration was of the following composition, and was made into pellets in a pelleting machine:

Bran	9·5 parts	Cod-liver oil	1·5 parts
White maize meal	24·3 ,,	Salt	0·5 .,
Meatings	24·3 .,	CaCO$_3$	2·5 .,
Sussex ground oats	24·3 .,	Dried milk	10·0 .,
Yeast	3·0 ,,		

The composition of the Sussex ground oats and white maize meal used was as follows:

	Sussex ground oats %	White maize meal %
Moisture	11·04	10·43
Protein	9·33	10·06
Ether extract	6·02	5·87
Fibre	9·01	2·55
Ash	2·60	1·64
Nitrogen-free extract	62·00	69·45

Water was usually given *ad libitum*, but intake was at times restricted to maintain a more or less solid character in the excreta.

Owing to limitations of staff it was not possible for the activity observations to be of the same exhaustive (and we may add exhausting) character as those described in paper II of this series. But the observer concerned with the metabolism measurements made a note of the activity at the time of each observation, and took observations, as far as might be, in such a manner as to include and allow for activity changes. That is to say, he adjusted his observation times to the activity of the bird. When it was quite still, observations might be made every 4 or 5 min., but immediately the activity changed another set of readings was taken, even though a set might have been recorded only a minute earlier. At the time of each observation of the metabolism the type of activity was also recorded on a simplified scheme of notation, so that an average figure could be obtained over half an hour on a system of point scores.

The correlation coefficient between change of activity and change of metabolism obtained from these notes was of course not so good as in the earlier tests mentioned but amounted to $+0.42$ and the coefficient of association for sign between the two was as follows:

Bird K	+ 0·64	Bird N	+ 0·15
,, L	+ 0·67	,, O	+ 0·68
,, M	+ 0·65		

Table I

Bird	Period	Dry matter feed g.	Energy of feed kg. cal.	Nitrogen of feed g.	Metabolizable energy kg. cal.	Dung nitrogen g.	Urinary nitrogen g.	Digestible energy kg. cal.	Digestibility coefficient of energy	Digestible nitrogen g.	Digestibility coefficient of nitrogen
K	Maintenance 1	83·6	378·0	2·166	261·7	0·397	1·262	273·6	72·4	1·769	81·7
	S.G.O. super.	157·2	726·7	3·384	493·3	0·632	2·042	512·6	70·5	2·752	81·3
	W.M.M. super.	199·9	640·2	3·129	462·4	0·607	1·883	480·2	75·0	2·522	80·6
	Maintenance 2	79·1	357·6	2·052	239·5	0·393	1·434	253·1	70·8	1·659	80·8
	S.G.O. super. – av. maintenance	75·9	358·9	1·275	242·7	0·237	0·694	249·3	69·5	1·038	81·4
	W.M.M. super. – av. maintenance	58·6	272·4	1·020	211·8	0·212	0·535	216·9	79·6	0·808	79·2
L	Maintenance 1	83·1	375·7	2·155	251·2	0·443	1·149	262·1	69·8	1·712	79·4
	S.G.O. super.	137·4	632·7	2·756	422·7	0·517	1·594	437·8	69·2	2·239	81·2
	W.M.M. super.	122·1	557·4	2·505	400·6	0·559	1·704	416·7	74·8	1·946	77·7
	Maintenance 2	79·5	359·4	2·064	238·8	0·378	1·364	251·7	70·0	1·686	81·7
	S.G.O. super. – av. maintenance	56·1	265·1	0·646	177·7	0·107	0·338	180·9	68·2	0·540	83·6
	W.M.M. super. – av. maintenance	40·8	189·8	0·395	155·6	0·149	0·448	159·8	84·2	0·247	62·5
M	Maintenance 1	71·6	309·4	1·843	208·3	0·426	1·334	220·9	71·4	1·417	76·9
	S.G.O. super.	136·6	615·5	2·924	402·2	0·602	2·003	421·1	68·4	2·322	79·4
	W.M.M. super.	122·6	548·5	2·735	393·6	0·559	1·751	410·2	74·8	2·176	79·6
	Maintenance 2	71·8	310·3	1·849	208·8	0·367	1·249	220·6	71·1	1·482	80·2
	S.G.O. super. – av. maintenance	64·9	305·6	1·078	193·6	0·206	0·712	200·3	65·5	0·873	81·0
	W.M.M. super. – av. maintenance	50·9	238·6	0·889	185·0	0·163	0·460	189·4	79·4	0·727	81·8
N	Maintenance 1	71·9	310·8	1·851	210·5	0·355	1·317	223·0	71·8	1·496	80·8
	S.G.O. super.	115·3	515·1	2·839	337·0	0·364	1·921	355·2	69·0	2·475	87·2
	W.M.M. super.	106·4	474·3	2·418	340·5	0·363	1·753	357·1	75·3	2·055	85·0
	Maintenance 2	71·2	307·7	1·833	202·4	0·319	1·577	217·3	70·6	1·514	82·6
	S.G.O. super. – av. maintenance	43·8	205·9	0·997	130·6	0·027	0·474	135·1	65·6	0·970	97·3
	W.M.M. super. – av. maintenance	34·9	165·1	0·576	134·1	0·026	0·306	137·0	83·0	0·550	95·5
O	S.G.O. super.	135·1	606·8	2·938	397·0	0·463	2·011	416·0	68·6	2·475	84·2
	W.M.M. super.	130·1	582·1	2·903	413·9	0·496	1·911	432·0	74·2	2·407	82·9
	Maintenance 2	77·3	334·1	1·989	217·6	0·364	1·641	233·1	69·8	1·625	81·7
	S.G.O. super. – maintenance	57·8	272·7	0·949	179·4	0·099	0·370	182·9	67·1	0·850	89·6
	W.M.M. super. – maintenance	52·8	248·0	0·914	196·3	0·132	0·270	198·9	80·2	0·782	85·6

The excreta were collected and weighed daily, and then combined into aggregates of 5 days each during maintenance and 4 days each during supermaintenance periods. These aggregates were preserved in the cold and mixed, sampled and analysed at the close of each 4- or 5-day period as the case might be.

The total energy of the excreta, and of the ration, was determined by a bomb calorimeter in a room kept at a constant temperature. The total nitrogen was estimated by the Kjeldahl method, the ammonia of the excreta by a modification of Foreman's method (Halnan, 1926), and the uric acid by a method devised by one of the writers (Hutchinson, 1940). For the calculation of the digestible energy and nitrogen Titus' (1928) modification of Katayama's factor (Katayama, 1924) was used for the dung N and Katayama's original factor for the organic matter in the urine. The methane production was not measured, since this is negligible in fowls.

During the period when the birds were not actually under test in the calorimeter they were kept in cages provided with the photoelectric recording apparatus; thus a fairly complete record of their activity during the test is available.

RESULTS

The results of the analyses of the excreta and the digestibility of the rations on a 24 hr. basis are given in Table I. The results of the calorimeter experiments are given in Table II. The figures in the columns headed "weighted average metabolism corrected to quiet sitting position" are obtained by applying a regression equation, computed from a correlation table drawn up from the results of the simpler activity observations made on this set of data, after giving suitable empirical values to the three or four positions noted, and weighting these according to the time for which they were maintained. The balance of energy was positive in all feeding periods.

If the feeding of the supermaintenance ration causes extra activity, then the energy required for this should presumably be reckoned as part of the thermic energy. On the other hand, if the changes in activity are fortuitous more accurate results might be obtained by correcting for it. Our evidence from the photoelectric cell records seems to show that the activity of the birds was approximately the same on all rations. The figures below give the number of hours standing out of the 24 with the different rations, when the birds were not in the calorimeter. The figures

Table II

Bird	Period	Date	Mean body wt. g.	Morning wtd. av. met. kg.cal. per 24 hr.	Afternoon wtd. av. met. kg.cal. per 24 hr.	Evening wtd. av. met. kg.cal. per 24 hr.	Night wtd. av. met. kg.cal. per 24 hr.	Dawn wtd. av. met. kg.cal. per 24 hr.	Mean wtd. av. met. kg.cal. per 24 hr.	Energy balance kg.cal. per 24 hr.	Mean wtd. av. met. corrected to "quiet sitting position" kg.cal. per 24 hr.
K	M_1	28. xi.–7. xii. 37	3803	242·2	205·7	228·4	197·1	203·6	215·4	+ 46·3	200·4
K	S_1 S.G.O.	12–17. xii. 37	4062	260·7	249·2	238·4	232·0	252·1	246·5	+ 246·8	233·6
K	S_2 W.M.M.	17–26. i. 38	3915	267·9	243·2	263·8	257·8}	245·7	254·1	+ 208·3	230·6
K	M_2	1–10. ii. 38	4071	264·4	232·4	207·0	242·4}	252·2	230·2	+ 9·3	219·8
L	M_1	28. xi.–7. xii. 37	3740	241·5	217·5	207·3	208·2	244·4	223·8	+ 27·4	208·8
L	S_1 W.M.M.	16–22. xii. 37	4002	275·5	264·6	246·7	229·4	240·2	251·3	+ 149·3	237·8
L	S_2 S.G.O.	16–25. i. 38	3855	283·1	248·9	258·4	247·6	245·4	256·7	+ 166·0	246·1
L	M_2	1–10. ii. 38	3988	297·6	221·3	232·5	188·3	234·5	234·8	+ 4·0	222·3
M	M_1	21–30. iii. 38	3039	163·3	120·4	127·5	133·3	132·3	135·3	+ 73·0	120·5
M	S_1 S.G.O.	4–11. iv. 38	3272	192·2	174·7	193·5	174·5	193·9	185·8	+ 216·4	171·1
M	S_2 W.M.M.	30. iv.–7. v. 38	3387	202·0	205·7	224·7	202·9	201·4	207·3	+ 186·3	194·5
M	M_2	12–21. v. 38	3410	188·4	165·9	177·6	156·2	166·0	170·8	+ 38·0	159·0
N	M_1	21–30. iii. 38	3049	156·3	137·3	144·2	126·8	146·6	142·2	+ 68·3	(130·3)
N	S_1 S.G.O.	26. iv.–l. v. 38	3276	181·5	175·1	168·1	147·6	196·5	173·8	+ 163·2	(161·0)
N	S_2 W.M.M.	23–30. v. 38	3221	199·4	179·5	164·2	170·5	201·3	183·0	+ 157·3	(172·7)
N	M_2	4–14. vi. 38	3263	199·4	154·0	165·0	165·5	180·8	172·9	+ 29·5	(158·0)
O	S_1 W.M.M.	4–11. iv. 38	3676	218·5	198·7	209·1	204·2	216·3	209·4	+ 204·5	198·2
O	S_2 S.G.O.	30. iv.–7. v. 38	3748	243·9	229·6	237·2	223·7	233·1	233·5	+ 163·5	219·4
O	M_2	12–21. v. 38	3781	216·2	203·9	206·4	187·9	177·2	198·3	+ 19·3	185·5

M_1 = First maintenance period. M_2 = Second maintenance period. S_1 = First supermaintenance period. S_2 = Second supermaintenance period. S.G.O. = Sussex ground oats. W.M.M. = White maize meal.

are the means of the observations on all birds on all days excluding the preliminary period.

Maintenance	All super. periods	Sussex ground oats super.	White maize super.
13·6	13·8	14·0	13·6

From these data it is clear that we have no evidence that any appreciable fraction of the thermic energy was produced by increased muscular exercise. As shown by Tables IV–VII given later in the paper the agreement between the individual values of the nett energy when corrected for activity is about the same as when uncorrected. The values themselves, as would be expected from the photoelectric cell data, are practically the same.

Table III. *Uric acid excretion and nitrogen balance in maintenance periods*

Bird	Basal 1 Uric acid N g./24 hr.	Basal 2 Uric acid N g./24 hr.	Basal 1 Nitrogen balance g./24 hr.	Basal 2 Nitrogen balance g./24 hr.
K	1·043	1·167	+0·507	+0·225
L	0·920	1·098	+0·563	+0·322
M	1·079	0·968	+0·083	+0·233
N	1·049	1·310	+0·179	-0·033

It will be noticed that all the birds which completed the whole series of feeding periods gave a higher metabolism in the second period of maintenance feeding than in the first, and irrespective of the order in which the supplements were fed the second supermaintenance period always gave results higher than the first. In the case of bird O there is no first maintenance period; this bird was brought into the experiment as a substitute for bird N when this latter broke its beak and went off its food, but again the second supermaintenance metabolism was higher than the first, and it appears not improbable from the general run of the results obtained with it, that had it been possible to complete the experiments on this bird, it would have presented a picture identical with that exhibited by the others.

Another point about this apparent rise in basal metabolism, or at all events in maintenance level of metabolism, is that it is considerably smaller in the case of birds K and L than in the other three. The only differences in treatment of these birds were that K and L were experimented on from November to February, and received spray dried milk in the basal ration, while M, N and O were experimented on from March to June and received roller dried milk which might have reduced the lysine content (Fairbanks & Mitchell, 1935), while only the cystine

content is reduced by spray drying. The cystine deficiency would presumably be made good by the cereals, but the lysine content would not. On the other hand, our basal ration contained nearly four times as much nitrogen as the endogenous requirements computed from the experiments of Ackerson *et al.* (1926). The uric acid excretion in the second basal period tended to be higher than in the first. Bird M, however, which gave a large rise in metabolism, excreted less uric acid in the second maintenance period, so that the difference can scarcely be regarded as significant. The differences in the nitrogen balance followed closely those in the uric acid excretion but in inverse sense. The figures are given in Table III.

Table IV. *Nett energy computed from interpolated values of maintenance metabolism*

1. Computation from unreduced values of heat production

	Sussex ground oats			White maize meal		
Bird	$\dfrac{\text{N.E.}}{\text{g. D.M.}}$ kg. cal.	$\dfrac{\text{N.E.}}{\text{M.E.}}$	$\dfrac{\text{N.E.}}{\text{D.E.}}$	$\dfrac{\text{N.E.}}{\text{g. D.M.}}$ kg. cal.	$\dfrac{\text{N.E.}}{\text{M.E.}}$	$\dfrac{\text{N.E.}}{\text{D.E.}}$
K	2·850	89·1	86·8	3·140	86·9	84·8
L	2·725	86·0	84·5	3·225	84·6	82·4
M	2·331	78·2	75·5	2·770	76·2	74·4
N	2·529	85·1	82·3	3·332	86·7	84·9
Mean	2·611	84·6	82·3	3·117	83·6	81·6

Table V

2. Computation from values of heat production reduced to "quiet sitting position"

	Sussex ground oats			White maize meal		
Bird	$\dfrac{\text{N.E.}}{\text{g. D.M.}}$ kg. cal.	$\dfrac{\text{N.E.}}{\text{M.E.}}$	$\dfrac{\text{N.E.}}{\text{D.E.}}$	$\dfrac{\text{N.E.}}{\text{g. D.M.}}$ kg. cal.	$\dfrac{\text{N.E.}}{\text{M.E.}}$	$\dfrac{\text{N.E.}}{\text{D.E.}}$
K	2·841	88·8	86·5	3·104	85·9	83·9
L	2·681	84·6	83·1	3·233	84·8	82·5
M	2·342	78·5	75·9	2·784	76·6	74·8
N	2·534	85·0	82·2	3·226	84·0	82·2
Mean	2·600	84·2	81·9	3·087	82·8	80·9

D.M. = dry matter; N.E. = nett energy; M.E. = metabolizable energy; D.E. = digestible energy.
Grand mean: S.G.O.   Nett energy = 10·291/4 = 2·573 cals./g.
              W.M.M. Nett energy = 12·191/4 = 3·048 cals./g.

A similar rise in basal metabolism has been observed recently by Kriss & Smith (1937) in rats. These experiments, however, refer to rats maintained for 3 months or so on a diet very deficient in minerals compared with others fed the same ration with the addition of 4% of Osborne and Mendel's salt mixture. They were able to satisfy themselves

that the rise which took place was attributable solely to an increase in basal metabolism.

Benedict & Ritzmann (1935) found spontaneous variations, in the endogenous basal heat production of fasting dry cows amounting to anything from 10 to 90%. Four cows showed 35–85% variation within 2 months. They found these changes to be affected by a change from hay to pasture feeding in the previous period. On the other hand, fluctuations of this order have never been found in experiments on cows published by other workers when the animals were being fed in nett energy experiments. If such changes did occur it would be impossible to determine the nett energy accurately.

Table VI. *Nett energy computed from mean of maintenance feeding periods "using different birds". Computation from unreduced values of heat production*

	Sussex ground oats				White maize meal		
	N.E. g. D.M. kg. cal.	N.E. M.E %	N.E. D.E. %	Bird	N.E. g. D.M. kg. cal.	N.E. M.E. %	N.E. D E. %
Bird							
K	2·885	90·2	87·8	L	3·275	85·9	83·6
L	2·679	84·6	83·1	K	3·080	85·2	83 2
M	2·479	83·1	80·3	O	3 117	83·9	82·8
O	2·138	68·9	67·6	M	2·570	70·7	69·1
Mean	2·545	81·7	79·7	Mean	3·011	81·4	79·7

D.M. − dry matter; N.E. = nett energy; M.E. = metabolizable energy; D.E. = digestible energy.

Table VII. *Computation from values of heat production reduced to "quiet sitting position"*

	Sussex ground oats				White maize meal		
	N.E. g. D.M. kg. cal.	N.E. M.E. %	N.E. D.E. %	Bird	N.E. g. D.M. kg. cal.	N.E. M.E. %	N.E. D.E. %
Bird							
K	2·888	90·3	87·9	L	3·267	85·7	83·4
L	2·622	82·8	81·3	K	3·027	83·8	81·8
M	2·499	83·8	81·0	O	3·053	82·1	81·0
O	2·130	68·6	67·3	M	2·558	70·4	68·7
Mean	2·535	81·4	79·4	Mean	2·976	80·5	78·7

D.M − dry matter; N.E. — nett energy; M.E. = metabolizable energy; D.E. = digestible energy.

The rise in metabolism we have observed could not be due to the fact that the birds were fatter in the second maintenance period than in the first. For the second *supermaintenance* metabolism was uniformly higher than the first, whichever ration was fed first, whereas on any mass

action theory, owing to the interposition of the weight adjustment period, it would be expected to be the same, so long as both supplements contained the same amount of thermic energy. We appear therefore to have to deal with a more or less steady rise in the maintenance metabolism.

If the cause of this rise in metabolism is dietary, then some departure from the fundamental principles enunciated by Møllgaard and others has taken place, in that the basal ration is not balanced so as to contain an optimum quantity of the various indispensable nutrients. This must be taken into account in interpreting the results. It is generally considered that the amino acid deficiencies of cereals are approximately the same, and Mitchell & Smuts have shown that the first deficiency of both oats and maize is lack of lysine (Mitchell & Smuts, 1932). It is unlikely therefore that a slight deficiency of essential amino acids would alter the comparative values obtained for the two cereals.

Recent work by Forbes (1932 and other papers) suggests that for the ruminant this optimal balance of nutrients is not yet fully understood, and it may even be that there are some nutrients which increase the thermic energy as a percentage of the metabolizable energy in whatever quantities they are introduced. Møllgaard (1929), in his attempts to devise an optimum basal ration for the measurement of the nett energy for fattening, has confined his attention to the level of protein, on the assumption that a normal mixed ration will be correctly balanced with respect to the other constituents, but Forbes' work seems to show that the position is more complicated. This has led both Forbes (1932) and Axelsson (1939) to doubt the value of attempts to measure the nett energy value of individual feeding-stuffs. As far as poultry and one-stomached animals are concerned, where there are less complications due to fermentation in the digestive system. the limits within which the constituents of a ration should be balanced are probably fairly wide. though the content of the more obscure B vitamins can easily be inadequate in experiments on growing animals. Nevertheless in view of the fact that the composition of an ideal basal ration is not accurately known, it may be that, in future, comparisons of feeding-stuffs should be made with a number of different basal rations. This principle is to some extent fulfilled in the present investigation, in that different quantities of the cereals under investigation were added to the basal ration, so that the supermaintenance rations vary in composition in individual experiments. Also, both roller and spray dried milk were used in the basal rations. It is possible, nevertheless, that a more rigorous

application of this principle would have improved the validity of our comparison of Sussex ground oats and white maize meal.

Taking into account this rise in metabolism, there appeared to be two methods by which the nett energy could be computed. We could assume that the rise is steady, and interpolate the maintenance value of the heat production for each supermaintenance period, using for this calculation birds K, L, M and N, and comparing the nett energy of each
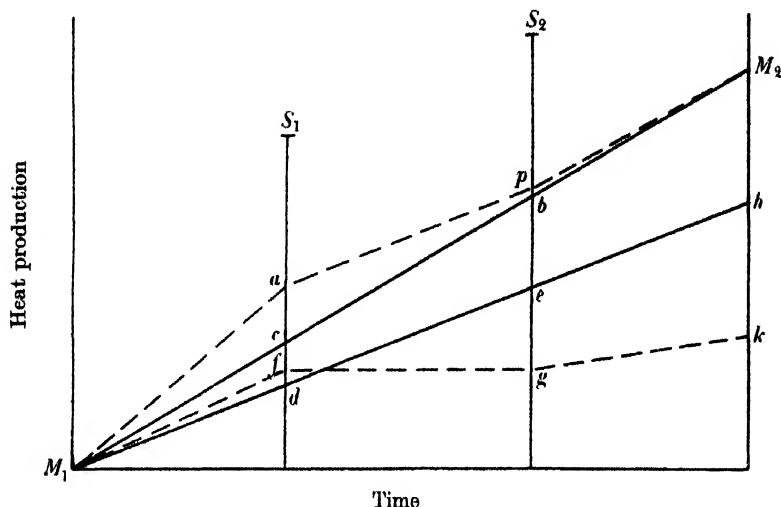

Fig. 1

cereal determined on the same bird. There might be some error in this procedure because part of the rise in metabolism would be caused by the fact that the birds were somewhat heavier in the second maintenance period. The position of affairs is shown in the diagram (Fig. 1).

M_1, S_1, S_2, M_2 are the heat production observed in the first maintenance, first supermaintenance, second supermaintenance and second maintenance periods respectively.

M_1cbM_2 is the trend of the maintenance metabolism as interpolated in the computation of nett energy.

M_1fgk is the effect of the changes in body weight in increasing maintenance metabolism throughout the experiment. The effect is greater between the first maintenance and first supermaintenance periods than between the second supermaintenance and second maintenance periods, because there were 4 days' preliminary supermaintenance feeding between the first two periods.

M_1deh represents a steady rise of the heat production of maintenance caused by some other factor than body weight.

$M_1 ap M_2$ is the combined effect of $M_1 deh$ and $M_1 fgk$, and represents the real trend of the maintenance metabolism.

The true thermic energy in the first supermaintenance period is thus $S_1 a$ and not $S_1 c$ as observed. Thus the nett energy as observed is too low in the first supermaintenance period. Since the Sussex ground oats ration was fed first in three out of four cases, there might be a bias in the comparative nett energy values from this cause.

If, however, the rise in metabolism is caused by some dietetic factor which increases the thermic energy of both the maintenance and supermaintenance rations, the nett energy of the supplement fed second might be relatively too low, and there would thus be an error in the opposite direction.

The alternative method is to take the mean of the metabolism in the two maintenance periods as the measure of maintenance metabolism. If the results obtained from the two rations on each bird are compared, the ration which is fed first naturally always gives the higher nett energy value. We have therefore compared the nett energy values obtained from pairs of birds which received different supermaintenance rations at the same time, while they also performed their maintenance periods at the same times, that is birds K, L, M and O. Bird O had only one maintenance period and the hypothetic heat production in the first maintenance period has therefore been computed from the results on bird M on the assumption that the rise in metabolism was of the same order as that of bird M which was determined at the same time. Any error in this assumption would alter the *variance* of the comparative nett energy values of the two cereals, but calculation of the results of the experiment on the assumption that no rise in maintenance metabolism occurred, which is clearly not the case, leaves the comparative nett energy values practically unchanged.

Tables IV–VII show the nett energy calculated by each method from the heat production both unreduced and reduced to the "quiet sitting position". The nett energy is expressed per gram dry matter of the feeding-stuff, as a percentage of the metabolizable energy, and as a percentage of the digestible energy. Both methods of calculation give practically the same results, using both the reduced and unreduced values of the heat production. The small size of the deviations of the differences between the two cereals in individual experiments is especially noteworthy. It is clear that there is no average difference between the two cereals exceeding about 3 % in the nett energy expressed as a percentage of the metabolizable energy. 82·5 % of the metabolizable energy was utilized

The mean values of the nett energy per gram dry matter of feeding-stuff were 2·573 kg. cals. for Sussex ground oats and 3·048 kg. cals. for white maize meal. It appears that, quite contrary to popular conception in this country, the white maize has a considerably higher nett energy value per gram of feeding-stuff. The cause of the difference is the higher digestibility of the energy of white maize meal, the average digestibility of which was 81·3 %, while that of Sussex ground oats was 67·2 %. The digestibilities are computed from difference experiments, and any associative effect of the digestibilities of the cereals and the basal rations is included in the digestibility coefficients of the cereals.

Axelsson (1937) has put forward the hypothesis that the digestibility of feeding stuffs for poultry depends chiefly on their fibre content, but this phenomenon would not necessarily produce associative effects between the digestibility of cereals and that of other constituents of the rations with which they are normally fed. If it should turn out that there are associative effects, then the comparative value of the two cereals would vary according to the basal ration with which they are fed. The basal ration in these experiments was, however, designed to be optimal in its balance of nutrients, so that presumably the digestible energy of the two cereals should be near its maximum under these conditions as well as the thermic energy being at a minimum. There is a good deal of variation in the digestibility of different varieties of oats (Halnan, 1926), so that the nett energy per gram dry matter of different types will vary within fairly wide limits.

The percentage of the total energy deposited as protein was 7·5 for Sussex ground oats and 2·8 for white maize meal, as computed from birds K, L, M and N. Hence the nett energy measured must represent almost exclusively nett energy for fattening. Rather more protein was laid down on the Sussex ground oats ration, which contained more digestible nitrogen than the white maize meal.

The only other determination of the nett energy value of a cereal for fowls is that of Mitchell & Haines. They determined the nett energy of yellow maize for maintenance on Rhode Island Red cocks and hens (Mitchell & Haines, 1927), and found that 84·7 % of the metabolizable energy was utilized. This is slightly higher than our value, but by analogy with the cow, which utilizes much more of the metabolizable energy for maintenance than for fattening, the difference would be expected to be greater still. Mitchell's ration, however, consisted solely of yellow maize and may not have contained the optimum balance of nutrients. He found that 83 % of the energy of the maize was metabolizable as com-

pared with our figure of 79·5 % for white maize meal obtained at a higher plane of nutrition. The utilization of metabolizable energy for cereals by fowls is higher than that of 70–80 % reported for the pig by most workers on various rations. The few figures reported for cereals on pigs are very variable, but Fingerling (1933) has obtained a value as high as 87·7 % for barley. Our figure of 82·5 % is also higher than the values for yellow maize of 56–74 % found by Forbes and co-workers for cattle (1928, 1930). It seems possible from the very meagre data available that the fowl counterbalances a lower digestibility of the food as compared with other farm animals by a higher utilization of the metabolizable energy.

Southgate (1930) has determined the nett energy per gram feeding-stuff for maintenance and fattening of a ration of Sussex ground oats and dried milk in the proportion oats : milk = 13 : 3, and the maintenance requirements of Light Sussex cockerels by a comparative slaughter method. The birds were fed by cramming. His value for the nett energy was 1·8 kg. cals./g. dry feed, that is 2·01 kg. cals./g. dry matter, much lower than our value for Sussex ground oats of 2·573 kg. cals./g. His method of calculation is based on the assumption that the nett energy is constant over a very wide range of plane of nutrition. This assumption is arbitrary, and his experimental results do not justify it. One of us (J. C. D. H.) has recomputed the nett energy at different planes of nutrition from his figures after correcting the gain of energy for the differences in surface area of the birds, using for this correction the figure for the maintenance requirements in nett kg. cals. per square metre surface area given by Southgate. Our computation is given in the following table. The plane of nutrition is given in multiples of the food requirement for maintenance interpolated from the energy balances above and below maintenance, since there were no figures for a state of energy equilibrium. The nett energy between 1·7 × maintenance and 1 × maintenance is also calculated from an interpolated value for the food intake necessary for maintenance.

Plane of nutrition	Nett energy, kg. cal. per g. dry matter
1·3 × M–0·7 × M	3·68
1·7 × M–1 × M	1·78
3·3 × M–1·7 × M	1·67

If these figures mean anything it would appear that cramming causes a great decrease in nett energy above the maintenance level of nutrition. It should be pointed out, however, that there is no estimate of the accuracy of Southgate's figures. In this connexion Halnan's work on

the normal variations in the composition of Light Sussex cockerels (1938*b*) shows that very large errors are possible in the comparative slaughter method. He found that the standard deviation of the energy content per 100 g. live weight was 11·42% of the energy content. This means that in a determination of the nett energy with two groups of fourteen birds each over a 14-day feeding period, when the nett energy is measured as the difference in final energy content between one group fed at a maintenance level and the other group at a 2 × maintenance level, the standard error of the mean nett energy value would be of the order of 9%. This standard error is the error in the assumption that two groups of birds having the same live weight at the beginning of the experiment have also the same initial energy content. It is in addition to the other errors in the experiment caused by differences in the reactions of the individual birds to the rations, and to errors in the calculation of the correction for increase in body weight on the supermaintenance ration. Southgate used only eighteen birds altogether divided amongst four planes of nutrition.

Halnan (1938*a*) has also determined the energy gain of cockerels fattened on Sussex ground oats with the addition of different quantities of dried milk, but has made no estimate of the maintenance requirements.

Axelsson (1937) has suggested that the energy value of rations should be computed from the digestibility coefficients of the protein, fat, and nitrogen free extract, and gives factors to convert the digestible nutrients into metabolizable energy. Assuming that his factors are correct, Axelsson's system depends upon the assumption that the utilization of the metabolizable energy of all feeding-stuffs is the same when they are combined in balanced rations. As far as the cereals are concerned our experiments seem to support such a system. For since there is no difference in the utilization of the metabolizable energy of Sussex ground oats and white maize meal, the reputed best and worst cereals, there is hardly likely to be any difference between these and other cereals. More information is needed on the nett energy values of the other components of a ration, in particular that of nitrogenous concentrates, but in any practical ration the cereal products provide a great proportion of the energy, except where fat in some form is added to fattening rations. Furthermore the quantities of other constituents are usually fixed by other considerations than their energy value.

It appears from these experiments that differences in fibre content between feeding stuffs have no influence on the utilization of metabolizable energy, so long as the fibre content of rations containing them is within ordinary physiological limits. For the Sussex ground oats

contained considerably more fibre, and probably also more pentosans, judging from the analyses of Fraps (1931), than the white maize meal. Axelsson (1937) has computed, from the experiments of other investigators, the utilization of "nitrogen-free" metabolizable energy for maintenance and egg production, and finds that variations in the fibre content of the rations within physiological limits do not affect it. In some of the experiments he cites the birds were kept on range, and he does not state that any allowance is made in the metabolizable energy for food picked up. Axelsson calculates the nett energy from standard maintenance requirements for energy which he has worked out; it would not necessarily be correct for individual experiments in which the birds were kept under widely differing conditions.

From Tables IV-VII we can get some idea of the variations of the nett energy, as measured on different birds, compared with the corresponding variations when the nett energy is measured twice on the same bird. We have used for this comparison the nett energy divided by the metabolizable energy calculated on the unreduced values of the heat production from the interpolated maintenance values using birds K, L, M and N. We have, then,

	Degrees of freedom	Squares	Mean squares	$\frac{1}{2} \log e$
Between rations	1	2·00	2·00	0·3466
Within birds	3	4·68	1·56	0·2223
Between birds	3	135·00	45·00	1·9034
	7	141·68	20·24	

z for the difference in variance within birds from that between birds is 1·681. From the tables of z the figure for 1 % significance is 1·692, so that the difference is significant. It must be remembered, however, that the basal ration of birds M and N was different from that of K and L in that it contained roller-dried milk in place of spray dried milk, and that L and N were at a slightly lower plane of nutrition than K and M. These factors may have increased the variance between birds. From the mean squares within birds we can calculate that to detect a difference between rations it would be necessary to have a difference of 2·8 % in the

$$\frac{\text{nett energy}}{\text{metabolizable energy}} \text{ for a significance of } 5\%.$$

Fig. 2 gives the $\dfrac{\text{nett energy}}{\text{metabolizable energy}}$ and $\dfrac{\text{metabolizable energy}}{\text{feed energy}}$ as functions of the plane of nutrition as expressed by

$$\frac{\text{metabolizable energy}}{\text{maintenance heat production}}.$$

The values of $\dfrac{\text{metabolizable energy}}{\text{feed energy}}$ are the mean of the results on the

two cereals for each bird. The $\dfrac{\text{nett energy}}{\text{metabolizable energy}}$ is computed on the

unreduced values of the heat production by the interpolation method. There seems to be a slight tendency for the metabolizable energy per gram feeding-stuff to diminish as the plane of nutrition is raised, in agreement with Forbes and co-workers' experiments on steers (1928, 1930). Halnan (1928c) has also investigated the effect of plane of nutrition
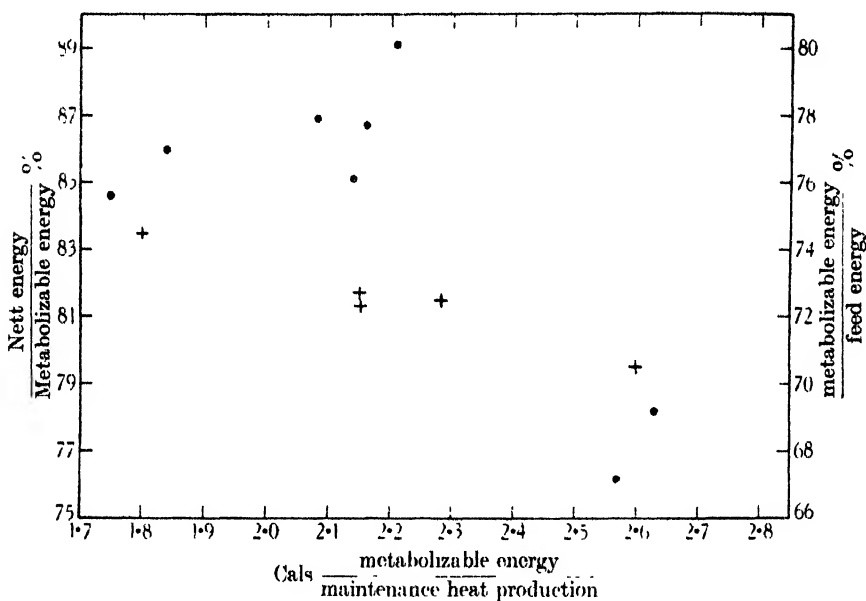

Fig. 2. Effect of plane of nutrition on $\dfrac{\text{nett energy}}{\text{metabolizable energy}}$ and $\dfrac{\text{metabolizable energy}}{\text{feed energy}}$.

$\bullet = \dfrac{\text{nett energy}}{\text{metabolizable energy}}$ $\quad + = \dfrac{\text{metabolizable energy}}{\text{feed energy}}$

on the digestibility of the organic matter of a ration of Sussex ground oats and skim milk. The digestibility decreased slightly from 69·3 to 67·3 % when the food intake was raised from 50 to 150 g. per diem. His figures are in good agreement with ours. Our results are not sufficiently

accurate to show any small change in the $\dfrac{\text{nett energy}}{\text{metabolizable energy}}$ with

increasing plane of nutrition, but it is clear that if such an effect exists it must be small. To demonstrate such an effect it would be necessary to make absolutely certain that the balance of nutrients is optimal at all planes of nutrition, that the weight correction could not have any

influence on the results, and to perform a sufficient number of experiments at different levels to get an estimate of their accuracy.

Since this paper was prepared for publication Fraps & Carlyle (1939) have reported the results of nett energy experiments with growing chicks on maize and various wheat products. They find a large difference in the utilization of the metabolizable energy of the different cereal products. Their values range from 61% for maize to 41% for wheat bran. Their calculation of nett energy is complicated and depends on various assumptions. The values deduced for the utilization of metabolizable energy are dependent on these assumptions, but there do appear to be differences between the values for different cereals whatever reasonable assumptions are made in the calculation of nett energy. There seem to be two possible explanations of the discrepancy between their results and ours. Either there are differences in the utilization of the metabolizable energy from different sources for growing chicks but not for fattening adult birds, or their basal ration was not of such a composition that the different cereal products were able to exhibit their maximum nett energy values.

SUMMARY

1. The comparative nett energy for fattening of Sussex ground oats and white maize meal have been determined on Light Sussex cockerels by difference experiments with a direct calorimeter.

2. The mean values for nett energy per gram dry matter, nett energy/ metabolizable energy, metabolizable energy per gross feed energy and digestible energy per gross feed energy were as follows:

	Sussex ground oats	White maize meal
Nett energy per gram dry matter	2·573 kg. cal.	3·048 kg. cal.
Nett energy - metabolizable energy	83%	82·1%
Metabolizable energy - gross feed energy	65·4%	79·5%
Digestible energy - gross feed energy	67·2%	81·3%

3. There was no significant difference in the utilization of metabolizable energy from the two cereals. The higher nett energy of the white maize meal was due to its higher digestibility.

REFERENCES

ACKERSON, C. W., BLISH, M. J. & MUSSEHL, F. E. (1926). *Poult. Sci.* **5**, 153.

AXELSSON, J. (1937). *Lantbrukshögskolans Annaler*, **4**, 131.

—— (1939). *Seventh World's Poultry Congress and Exposition, Proc.* p. 165.

BAROTT, H. G., FRITZ, J. C., PRINGLE, E. M. & TITUS, H. W. (1938). *J. Nutrit.* **15**, 145.

BENEDICT, F. G., LANDAUER, W. & FOX, E. L. (1932). *Bull. Storrs agric. Exp. Sta.* No. 177.

BENEDICT, F. G. & LEE, R. C. (1937). *Publ. Carneg. Instn*, No. 489.

BENEDICT, F. G. & RITZMAN, E. G. (1935). *Proc. nat. Acad. Sci. Wash.* **21**, 304.

DEIGHTON, T. (1939). *J. agric. Sci.* **29**, 431.

DEIGHTON, T. & HUTCHINSON, J. C. D. (1940). *J. agric. Sci.* **30**, 141.

FAIRBANKS, B. W. & MITCHELL. H. H. (1935). *J. agric. Res.* **51**, 1107.

FINGERLING, G. (1933). *Versuchstationen.* **116**, 1.

FORBES, E. B., BRAMAN, W. W. & KRISS, M. (1928). *J. agric. Res.* **37**, 253.

—— —— —— (1930). *J. agric. Res.* **40**, 37.

FORBES, E. B. (1932). *Proc. Amer. Soc. Anim. Prod.* Annual Meeting, p. 32.

FORBES, E. B., SWIFT, R. W., BLACK, A. & KAHLENBERG, O. J. (1935). *J. Nutrit.* **10**, 461.

FRAPS, G. S. (1931). *Bull. Tex. agric. Exp. Sta.* No. 437.

FRAPS, G. S. & CARLYLE, E. C. (1939). *J. Nutrit.* **18**, 385.

HALNAN, E. T. (1926). *J. agric. Sci.* **16**, 451.

—— (1928a). *J. agric. Sci.* **18**, 421.

—— (1928b). *J. agric. Sci.* **18**, 634.

—— (1928c). *J. agric. Sci.* **18**, 766.

—— (1938a). *J. agric. Sci.* **28**, 341.

—— (1938b). *J. agric. Sci.* **28**, 379.

HAMILTON, T. S. (1939). *J. Nutrit.* **17**, 583.

HUTCHINSON, J. C. D. (1940). *Biochem. J.* (In press.)

KATAYAMA, T. (1924). *Bull. imp. agric. Exp. Sta. Japan*, **3**, no. 1.

KRISS, M. & SMITH, A. H. (1937). *J. Nutrit.* **14**, 487.

MITCHELL, H. H. & CARMAN, C. G. (1924). *J. biol. Chem.* **60**, 613.

MITCHELL, H. H. & HAINES, W. T. (1927). *J. agric. Res.* **34**, 927.

MITCHELL, H. H. & SMUTS, D. B. (1932). *J. biol. Chem.* **95**, 263.

MØLLGAARD, H. (1929). *Fütterungslehre des Milchviehs.* Hannover (Schaper).

MØLLGAARD, H. & THORBEK, G. (1938). *Tierernährung*, **10**, 105.

SOUTHGATE, B. A. (1930). *J. agric. Sci.* **20**, 206.

TITUS, H W. (1928). *Poult. Sci.* **7**, 145.

WASTAGE, LENGTH OF PRODUCTIVE LIFE, REPLACEMENT AND DEPRECIATION OF DAIRY COWS

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(With Three Text-figures)

THIS paper is based upon information and experience obtained during the three-year period 1934–5 to 1936–7 in the operation of the Cambridge Food Recording Scheme for Dairy Cows. The Scheme, which is an advisory service to milk producers in the Eastern Counties, has a broader basis than its name suggests, and is, in fact, a general study of the economic aspects of milk production. Attention is concentrated upon the quantitative, rather than purely monetary, presentation of results, and this is especially so in the present paper.

The members of the Scheme are drawn from various parts of the Eastern Counties, but all are engaged in production for the "liquid" milk market. With very few exceptions they try to maintain a comparatively even supply throughout the year, average daily production per herd being only 7 % lower in winter than in summer.

WASTAGE AND LENGTH OF PRODUCTIVE LIFE

Wastage from dairy herds has been the subject of several investigations which will be referred to later. The main excuse for reopening the discussion is the unusually close supervision of the farmers' original records for which the present study provides. This eliminates what was a serious weakness of some preceding investigations, viz. the number of cows "lost" during the period studied. The present sample is, however, a special one, in that all the herds are milk-recorded, officially or privately, and as in the case of previous investigations it is only representative of a section, although an important section, of the dairying industry.

Over the three-year period 1934–5 to 1936–7, 249 "herd years" are available for the study of wastage and replacement, and have been combined in Table I:

Table I. *Summary of wastage and replacement during*
249 *"herd years"*

No. of cows in opening valuations		7700	No. of cows in closing valuations		7847
No. of heifers drafted in	1579		No. of cows sold or transferred out	1958	
No. of cows purchased	754		No. of cows died	228	
Total entry		2333	Total wastage		2186
		10,033			10,033

Annual wastage amounts to 28·4% of the number of cows included in the opening valuations: this is equivalent to a productive herd life of 3·5 years. During the period under discussion, size of herd was increasing at the rate of 2% per year, and it is reasonable to suppose that this increase was accompanied by a reduction in the normal rate of culling inferior cows. If it was due in equal measure to a subnormal rate of culling and to a higher than normal rate of entry, then corrected wastage would be 2259, which is 29·3% of the number of cows included in opening valuations. This is equivalent to a productive herd life of 3·4 years.

This estimate of average productive herd life is in substantial agreement with the findings of other workers. Sanders (1939), who obtained data through milk recording societies for 1572 "herd years", concluded that average productive herd life was 3·6 years. The National Institute for Research in Dairying (1933) obtained a figure of 3·2 years from similar data relating to 470 herds.

It must be remembered that a proportion of the cows disposed of from any one herd are purchased by other milk producers. Consequently, percentage wastage from the individual herd is greater than from all dairy herds collectively, and *herd* life is shorter than *total* life. In the present investigation it was not practicable to analyse total wastage into its components with a view to estimating the total productive life of the dairy cow.[1] Provision is made on the valuation forms, however, for a statement of the age of each cow in the herd in terms of "Number of times calved", which is the only practicable measure of age in the case of commercial cattle. The opening valuations of 125 different herds gave sufficiently full information to warrant analysis, and the ages of 3875 cows in these herds were distributed as in Table II.

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[1] Farmers co-operating in the investigation are required to supply so much "essential" information that it is not considered desirable to insist upon their supplying explanatory details as to reasons for the disposal of cows.

Wastage during the first and second lactations is evidently small, and 87·5% of cows reach the third calf group. Subsequently the rate of wastage is much greater, e.g. fourth calf cows are only 63·0% as numerous as third calvers. If it is assumed that the thirty-two cows in the "Unknown" group have had an average of five calves—a reasonable assumption, since the older the cow the more likely is its age to be in doubt—then average age in terms of number of times calved is 3·1, corresponding to a position approximately midway between third and fourth calvings.

Table II. *Age distribution of* 3875 *cows*

Age groups	No. of cows	No. as percentage of of total	No. as percentage of preceding age group
1st calvers	912	23·5	×
2nd ,,	870	22·5	95·4
3rd ,,	798	20·6	91·7
4th ,,	503	13·0	63·0
5th ,,	318	8·2	63·2
6th ,,	201	5·2	63·2
7th ,,	117	3·0	58·2
8th ,,	64	1·65	54·7
9th ,,	33	0·85	51·6
10th ,,	16	0·4	48·5
11th ,,	5		
12th ,,	2		
13th ,,	—	0·3	
14th ,,	3		
15th ,,	1		
Unknown	32	0·8	
Total	3875	100·0	×

If average length of total productive life is to be estimated from the data in Table II, arbitrary assumptions must be made as to average interval between calvings, and between latest calving and valuation. It will be assumed that these intervals are 1 year and 6 months respectively. Hammond (1927) averaged the interval between calving and fertile service of over 5000 milk-recorded cows and found it to be 97 days, which corresponds to an interval of 1 year and 12 days between full-time calvings. Applying the above assumptions to the data in Table II, it is found that for every 933[1] individuals which enter the milking herd the aggregate expectation of life (Tx of a life table) is 3843 years, and so average expectation of life is approximately 4·1 years.[2] Since the age

[1] Of these 933 individuals, 912 survive to be recorded as first calvers at an average of 6 months later.

[2] This assumes a stable population, while in actual fact it was slightly increasing at the time when the study was made. However, the introduction of a correction for this would not materially add to the accuracy of an admittedly approximate calculation.

distribution on which these calculations are based is in terms of total productive life, and not merely productive life in any one herd, it follows that average length of total productive life is approximately 4·1 years also.

Two other investigators have estimated average length of total productive life by reference to age distributions. Buchanan-Smith (1931) concluded from a study of the ages of the parents of 2600 pedigree calves that the figure was 3·7 years. Wright (1933) gives 3·6 years; his calculations were based on the age distribution of over 7000 high-yielding milk recorded cows. Both investigators appear to assume that in their samples actual average age was the same as average total length of life. This assumption is difficult to justify if the picture in Table II of a marked tendency for the wastage to be greater in the higher age groups is even approximately correct. It is highly probable, therefore, that both Buchanan-Smith and Wright under-estimated average length of life.

There is another method of estimating average length of total productive life. Both the National Institute for Research in Dairying (1933) and Sanders (1939) were able to analyse wastage into its components and to distinguish between *total* wastage and "*true*" wastage. They assume that cows disposed of under the headings of "Trade" and "Low Milk Yield" are sold into other dairy herds, and destined, therefore, to appear later in some category of "true" wastage. If their estimates of "true" wastage are used to calculate average length of total productive life, then the figures are: The National Institute for Research in Dairying, 4·7 years and Sanders, 5·8 years. The discrepancy between these estimates and those derived from the present investigation may be due to a peculiarity of the samples. In all the investigations the herds studied were milk recorded privately or officially. It is unlikely that such herds purchase a normal proportion of cows which are "throw-outs" from other herds. Most of these "throw-outs" probably pass on to herds having lower standards of production. If this is so, then calculations based upon analyses of wastage (The National Institute for Research in Dairying and Sanders) will over-estimate average length of total productive life, while calculations based upon age distributions (the present investigation) will under-estimate it.

SALES AND DEATHS

Sales of cows and transfers-out numbered 1958 and represented 89·6% of total wastage. The average sum realized for such cows was £11. 12s. per head.

Deaths of cows amounted to 228, equivalent to 10·4% of the total wastage, and to a mortality rate of 3·0% of the number included in opening valuations. The average sum realized for such cows was £1. 5s. This average was considerably enhanced by a few receipts from insurance companies on account of deaths due to lightning. Sanders (1939) found in a study of 1572 "herd years" of milk recording society members that 9·9% of the total cows disposed of died before they left the herd.

The overall average receipt for the 2186 cows which left the herds during the three-year period was £10. 10s. 6d. per head.

REPLACEMENT

During the three-year period 1934–5 to 1936–7, 2333 cows and heifers entered the herds. This is equivalent to a crude replacement rate of 30·3% of the number included in the opening valuations. After the application of the correction for increase in size of herd described above (p. 486) the figure becomes 29·3%.

Of the total of 2333 animals, 1579, or 67·7%, were first-calf heifers, and 754, or 32·3%, were cows. For the purposes of this investigation, the definition of "cow" is of a rather special nature. The instruction to co-operating farmers is that a "heifer" becomes a "cow" as soon as she has had her first calf. The average market value placed upon heifers when they entered the milking herd was £20. 14s. per head. Cows cost an average of £22. 5s. per head.

Because 67·7% of replacements were heifers, it does not follow that the same proportion was home-bred. An unknown proportion of the heifers was purchased as calves or at some subsequent stage prior to calving. In practice, when dealing with commercial herds, it is not always possible to obtain satisfactory classification into home-breds and purchases. It is possible, however, to obtain some information on the point from the valuations of 135 different herds.[1] Of a total of 4367 cows, 49·0% were described as home-bred, 50·6% as purchased and 0·4% as unknown.

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[1] A number of valuations in which no attempt was made at classification are excluded. It is not considered that inclusion of these herds, if the information were available, would substantially alter the results of the analysis.

Members' weekly returns, which formed the original data,[1] were adjusted to refer to calendar months, and subsequently to standard months of 30 days. These were then corrected so as to restore the overall totals for the year to the original figures.

Table III. *Seasonality of Herd Changes. 249 "Herd Years"*

Standard months	No. of cows purchased	No. of heifers drafted in	Total entry (heifers and cows)	Total wastage (sales, transfers out and deaths)	Total calvings
January	48	120	168	184	553
February	33	100	133	190	626
March	29	81	110	211	601
April	36	61	97	213	439
May	44	62	106	173	415
June	62	96	158	141	566
July	75	130	205	152	611
August	50	199	249	148	697
September	108	230	338	202	772
October	130	218	348	218	727
November	85	151	236	176	680
December	54	131	185	178	613
Total	754	1579	2333	2186	7300

Diagrams I, II and III are designed in graph form to illustrate variations in seasonality, figures for standard months being plotted as percentages of year totals. A policy of level milk production is characteristic of the herds in this study and is responsible for an autumn peak in entries to the herd. Diagram I shows that heifer entries are at a maximum in September and fall steeply after October to a minimum in April and May. The curve illustrating the entry of cows into the herd has a similar general form, but shows interesting differences of detail. The peak occurs later—in October instead of September—and is more sharply defined than the peak heifer entry, while the trough occurs earlier. In August, the otherwise continuous rise from March to October is broken by a sharp drop in purchases of cows, presumably due to a slack trade during harvest.

Diagram II compares the seasonality of total entry to the herd (cows and heifers) with that of wastage from it. Wastage shows less fluctuation

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[1] Some of the weekly returns necessarily include days of two different months. In such cases, the changes occurring during any particular week have been apportioned to the months concerned by reference to the number of days from each month which are included in the week in question. After completion of the analysis, it was found, by reference to the summary of wastage from the herd and replacement (see p. 486), that a small number of observations had been missed, equivalent to an overall average of 1 in 265. The errors were distributed over the months in the proportions of the monthly totals. Figures for "Total Calvings", which are not subject to the same check, were also increased by 1 in 265.
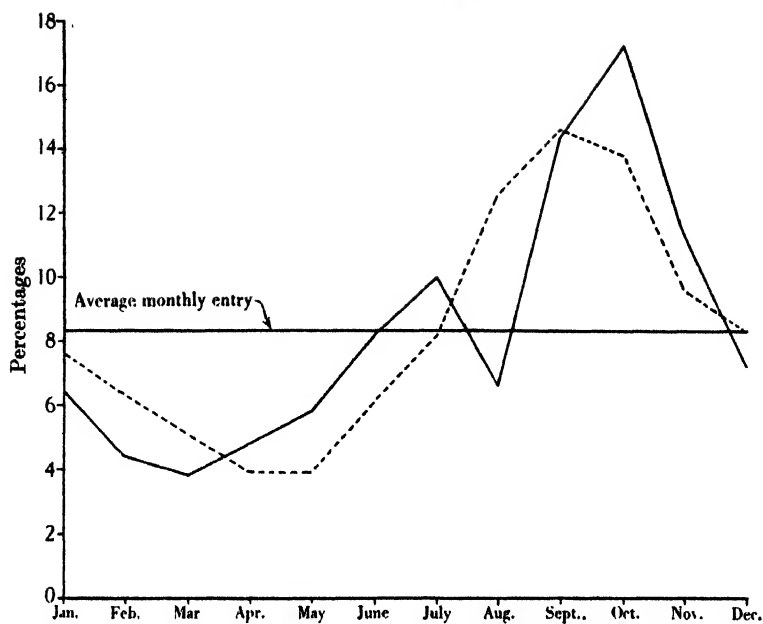
Diagram I.

————— Monthly cow entry as % of total cow entry.
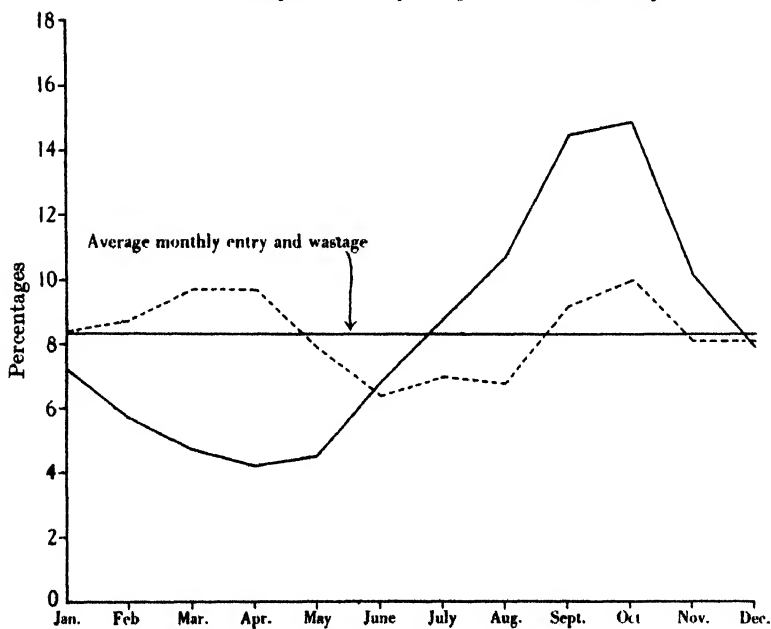- - - - - Monthly heifer entry as % of total heifer entry.

Diagram II.

————— Monthly entry as % of total entry.
- - - - - Monthly wastage as % of total wastage.

than replacement and the form of the curve is notably different. Wastage shows two peaks—one in March–April and the other in October. During the months of June to November inclusive entries into the herd exceed wastage, while from December to May inclusive the reverse holds true.

Diagram III shows how the distribution through the year of first calvings in the herd differs from that of total calvings. The seasonality of first calvings in the herd may be assumed to resemble closely that of entry into the herd. This is because heifers are drafted in at calving and
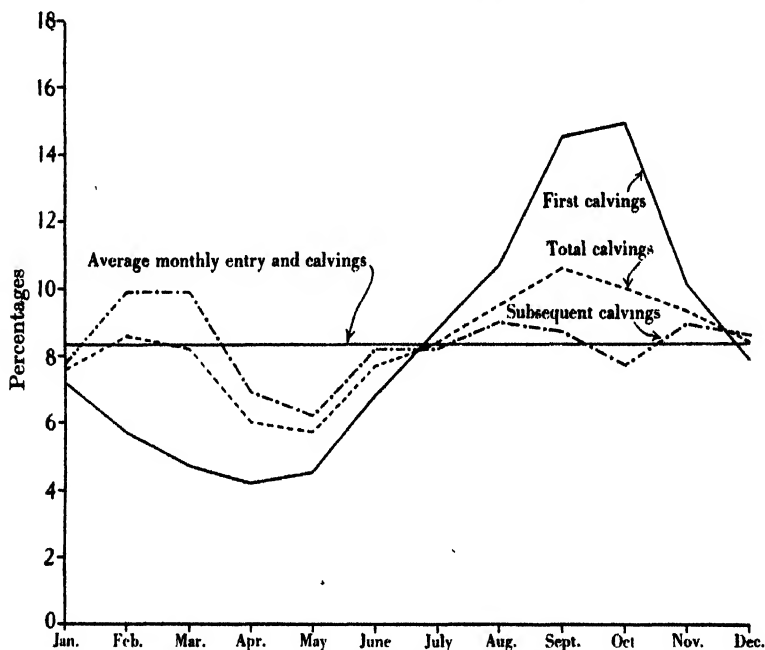

Diagram III.

——— Monthly entry as % of total entry
····· Monthly calvings as % of total calvings.
–·–·– Monthly calvings other than by new entries to herd, as % of all such calvings.

the majority of cows purchased are either down-calvers or freshly calved. The "first calvings curve" may, therefore, be assumed to show the same marked seasonality, with an October peak, as does the "entry curve". The curve of monthly calvings by cows which are *not* new entries to the herd shows very different characteristics. Seasonality is much less marked; there is no autumn peak, but there is a decided peak in February–March, which is absent from the "entry curve". The curve illustrating the seasonality of total calvings follows a course intermediate between the "first calvings curve" and the "subsequent calvings curve", and shows two peaks. The first is in September, and is due to the high pro-

portion of first calvings occurring then, while the second peak, in February–March, is due to the high proportion of "subsequent" calvings occurring at that time. Roberts (1929) studied the milk records of 950 Welsh Black cattle. He found that while only 17 % of first-calvers calved in March, April, May, the proportion was so high as 42 % in the case of sixth-calf cows.

The February–March peak in "subsequent" calvings corresponds to a peak in conceptions during May–June, which is, no doubt, associated with the all-round improvement at that time of year in the conditions making for fertility in the cow, viz. the change from winter indoor to summer outdoor conditions, and the early summer flush of grass. Marshall (1937) has shown the remarkable reaction of ruminants to seasonal changes, by reference to natural experiments in which animals, of varieties or species that normally breed once annually, have been shipped across the equator and as a consequence have been induced to have two sexual seasons in one year. The symptoms of heat are stronger and also more readily observed in summer than in winter, when the cows are tied up for most of the day and are left unattended for long periods. Furthermore, according to Hammond (1927) a heat period may sometimes be as short as 6 hr. in winter and as long as 30 hr. in summer, the average difference between the two extremes being 5–6 hr. It is not surprising, therefore, that many cows which have been temporarily sterile settle in calf during early summer. Such animals usually have an interval of more than a year between calvings. On the other hand, some cows calve again in less than a year, and Hammond shows that there is an optimum time during the months May–July when the reproductive force is at its maximum in the cow and that during November–January the reproductive powers are at a minimum. For these reasons "subsequent" calvings are more evenly distributed over the year than first calvings.

COST OF DEPRECIATION

Among the forty herds available as an identical sample for the three-year period 1934–5 to 1936–7 the average cost of depreciation per cow per year was £3. 5s., equivalent to 1·1d. per gallon. Figures will not be given for each year separately as it is unlikely that any significant trend could be observed over such a short period, particularly since the cost of depreciation in any one year is often greatly affected by a change in average valuation per cow. Over the three-year period, valuation changes almost cancel out. Actually, average valuation per cow was just over 5s.

per cow lower at the end of 1936–7 than at the beginning of 1934–5. If this fall is eliminated from the calculations, then average cost of depreciation per cow per year becomes £3. 3s., equivalent to 1·05d. per gallon.

The values of first-calf heifers when they enter the milking herd have often to be estimated, for many such animals are either home-bred or are purchased some considerable time before calving. The average value placed upon them over the three-year period was £20. 14s. Whilst this probably approximates to the actual market value, it is believed to be conservative rather than otherwise. Furthermore, although it is impossible to say what was the cost per head of rearing the heifers to calving, it is unlikely to have been less than the value placed upon them.

SOME FACTORS AFFECTING WASTAGE AND DEPRECIATION

For the study of factors affecting wastage, results are available from 129 different herds. In each case the latest available observation was chosen.

Table IV. *Herd size and wastage*

Range in herd size (cows)	No. of of herds	Average no. of cows in herd	Wastage of cows as a percentage of no. in opening valuations
Below 15	25	11	27·7
15–24½	32	20½	30·1
25–34½	30	30	28·4
35–44½	18	39½	30·1
45 and over	24	66	26·9
All together	129	32	28·6

It does not appear from Table IV that there is any connexion between size of herd and wastage.

Table V. *Milk yield per cow and wastage*

Range in milk yield per cow for the year (gallons)	No. of herds	Average yield per cow for the year (gallons)	Wastage of cows as percentage of no. in opening valuations	Estimate of "life-yield" per cow (gallons)
Below 500	8	474	26·3	1802
500–599	19	564	25·1	2247
600–699	41	654	30·4	2151
700–799	40	748	30·0	2493
800–899	13	843	26·5	3181
900 and over	8	1014	26·8	3784
All together	129	700	28·6	2448

There is no evidence from Table V of any simple relationship between level of milk yield per cow and rate of wastage. However, when the 129

herds are divided into low-yield and high-yield groups of equal size, the low-yield group is found to have a wastage of 27·9% and the high-yield group a wastage of 29·6%. A satisfactory explanation is not available of the rather high wastage shown by the groups of herds with yields of 600–699 and 700–799 gallons. From a series of analyses of New Zealand cow records, Ward (1939) concludes that it is difficult to find evidence that natural high production, as a sole cause, is responsible for any increase in the incidence of disease, or that such high production, of itself, increases a cow's susceptibility to disease.

For each yield group of Table V an estimated "life-yield" per cow has been computed from average yield per cow for the year and estimated length of herd life, based upon the rate of wastage. Since rate of wastage is not closely affected by level of milk yield, the estimated "life-yield" is almost directly dependent upon the latter. In the group having an average yield per cow for the year of 900 gallons and over, estimated "life-yield" is more than double that in the group with average yield per cow for the year below 500 gallons.

As has been explained on p. 493, only forty herds are available as an identical sample over the three-year period and, consequently, study of the relationship between milk yield per cow and cost of depreciation, as distinct from wastage, is limited to that number, less two herds omitted on account of marked abnormalities.

Table VI. *Milk yield per cow and depreciation*

Range in average milk yield per cow per year (gallons)	No. of herds	Average yield per cow per year (gallons)	Average depreciation per cow per year			Average depreciation per 100 gallons	
			£	*s.*	*d.*	*s.*	*d.*
Below 650	9	607	2	16	0	9	1
650–749	18	698	3	0	0	8	7
750 and over	11	854	3	11	8	8	6

It appears that depreciation per cow is greater among the higher yielding herds. On the evidence of Table V this can be due in only a small degree to a higher rate of wastage. It is accounted for by the higher values placed upon stock entering the higher yielding herds, and by the lower prices at which cast animals, being of more dairy type, leave them.

Depreciation per 100 gallons tends to be slightly lower among the higher yielding herds.

It is commonly believed that differences in the method of replacing the herd affect the rate of wastage from it. Herds replaced by home-bred stock are believed to have the better experience. As has been explained

on p. 489, satisfactory classification of replacements into home-bred and purchased is not practicable under the conditions of the investigation, and the alternative of calculating for each herd the proportions of the total entry contributed by heifers has been adopted.

Table VII. *Method of replacement and wastage*

Percentage of heifers in replacements	No. of herds	Heifer entry as percentage of total entry	Wastage of cows as percentage of no. in opening valuations	Estimate of "life-yield" per cow (gallons)
100	50	100	23·5	2928
50–99	44	73	31·3	2268
Below 50	29	21	34·7	2046

Six herds had no replacements

The herds replaced entirely by heifers clearly have the lower wastage. This is only to be expected, since a heifer has all its productive life before it, whereas a cow obviously has not. Estimated "life-yield" has been computed as in Table V.

SUMMARY

1. In the Eastern Counties of England, annual wastage from milk recorded dairy herds amounts to 29·3% of the number of cows at the beginning of the year.

2. Average length of productive *herd* life in milk recorded herds is 3·4 years.

3. Average length of *total* productive life in milk recorded herds is probably a little more than 4 years. Average length of *total* productive life in *all* herds is probably, longer, and may be of the order of 5 years.

4. Deaths of cows are equivalent to 10·4% of the total wastage, and to a mortality rate of 3·0% of the number of cows at the beginning of the year.

5. During the three-year period 1934–5 to 1936–7, cows leaving the herd realized an average of £10. 10s. 6d. per head. The average market value placed upon heifers when they entered the milking herd was £20. 14s. per head, while cows for replacement purposes cost an average of £22. 5s. per head.

6. Of all replacements, 67·7% are heifers, but not all of these are home-bred. In annual valuations, 49·0% of cows are described as home-bred, 50·6% as purchased and 0·4% as unknown.

7. Entries of heifers and purchases of cows both show a marked seasonality, and are at a maximum in September and October respectively.

Wastage is less seasonal. It is greatest in October, but almost as great in March and April.

8. First calvings are at a maximum in October, but "subsequent" calvings, which are more evenly distributed, are most frequent in February and March.

9. During the three-year period 1934–5 to 1936–7, the average cost of depreciation was £3. 5s. per cow in the herd per year, equivalent to 1·1d. per gallon.

10. Little connexion is found between size of herd and wastage or between milk yield per cow and wastage. However, the *cost* of depreciation per cow is considerably greater among the higher yielding herds, while depreciation per 100 gallons is slightly less.

11. Herds replaced entirely by heifers show the lowest wastage.

REFERENCES

BUCHANAN-SMITH, A. D. & ROBISON, O. J. (1931). *J. agric. Sci.* **21**, 136.

HAMMOND, J. (1927). *The Physiology of Reproduction in the Cow.* Cambridge University Press.

MARSHALL, F. H. A. (1937). *Proc. roy. Soc.* B, **122**, 413.

Nat. Inst. Res. Dairying, Reading (1933). *Yearb. Berks Milk Rec. Soc. 1933.*

ROBERTS, E. J. (1929). *Welsh J. Agric.* **5**, 67.

SANDERS, H. G. (1939). Report on the Scheme for Enquiry into the Causes of the Removal of Cows from Dairy Herds. Personal communication.

WARD, A. H. (1939). *Emp. J. exp. Agric.* **7**, 350.

WRIGHT, N. C. (1933). *Scot. J. Agric.* **16**, 131.

THE MOVEMENT OF POTASSIUM IN IRRIGATED AND FERTILIZED RED SANDY CLAY*

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(With Two Text-figures)

AIM OF EXPERIMENTS

THE present investigation was intended to furnish information concerning:

(1) The movement of water-soluble and exchangeable potassium in the soil profile after successive fertilizer applications.

(2) The form of potassium—exchangeable, soluble, or non-exchangeable—into which added potassium fertilizer is converted in the soil.

(3) The effect of doubling the fertilizer ration on the absorption of potassium by the soil; and the effect of doubling the ration of irrigation water on the absorption and accumulation of potassium in the soil.

(4) The effect of frequent successive summer irrigation following fertilizer application on the distribution of the three forms of soil potassium.

(5) The effect of fertilization followed by irrigation on soil pH value.

PLAN OF THE INVESTIGATION

The plot of land selected for the site of the experiment had not been cultivated or fertilized for many years. The soil was light red sandy clay lacking in calcium carbonate, of poor nutrient value, but of excellent physical characteristics.

The fallow land was marked off into equal plots of 3 by 3 m., and ten plots which appeared to be most uniform in physical properties were selected for the actual experiment. Growth of plants on the test soil plots was not permitted.

Fertilization and irrigation

Potassium fertilizer was applied as potassium sulphate which contained 49·8 % K_2O calculated to a basis of dry weight.

The experiment was continued over a period of three years and was marked by two stages: (a) the fertilization stage, which lasted two years, and (b) the irrigation stage, which followed the fertilization and continued through the summer.

The potassium fertilizer was applied in half-yearly rations, in spring on moist soil and again at the end of summer when soil moisture is very low. By this means it was hoped (a) to keep the conditions of the experiment reasonably close to those prevailing in practice, (b) to prevent the occurrence of sudden radical chemical changes in the soil due to the addition of overlarge quantities of fertilizer, and (c) to allow an average result unaffected by special environmental factors prevailing at the time of fertilizer application, e.g. soil moisture and temperature which have been shown by Kolodny & Joffe to affect soil adsorption of potassium.

The plots were paired as indicated in Table 1.

Table I. *Fertilization and irrigation system*

Serial no. of plot		Fertilizer (K_2SO_4 in g.) and irrigation (cu.m. water) applied in				
		November 1935	May 1936	November 1936	March 1937	Total
G2; G3	K_2SO_4	400	500	500	500	1900
	water	1·5	1·0	1·0	1·0	4·5
G4; G5	,,	400	500	500	500	1900
	,,	2·5	2·0	2·0	2·0	8·5
H1; H2	,,	800	1000	1000	1000	3800
	,,	1·5	1·0	1·0	1·0	4·5
H3; H4	,,	800	1000	1000	1000	3800
	,,	2·5	2·0	2·0	2·0	8·5
I1	water	1·5	1·5	1·5	1·5	6·0
K1	,,	2·5	2·5	2·5	2·5	10·0

Serial no. of plot	Rainfall 1935–6 mm.	Rainfall 1936–7 mm.	Irrigation cu.m. water applied in				
			May 1937	June 1937	August 1937	September 1937	October 1937
G2; G3	400	585	1·0	1·0	1·0	1·0	1·0
G4; G5	400	585	2·0	2·0	2·0	2·0	2·0
H1; H2	400	585	1·0	1·0	1·0	1·0	1·0
H3; H4	400	585	2·0	2·0	2·0	2·0	2·0
I1	400	585	1·5	1·5	1·5	1·5	1·5
K1	400	585	2·5	2·5	2·5	2·5	2·5

At the end of two years the fertilizer experiment entered on the irrigation stage. Accordingly in summer 1937 watering was carried out five times at intervals of six weeks.

Water-soluble potassium was separated by shaking the soil in 5 parts water for 2 hr. Exchangeable potassium was determined by extraction of 12·5 g. soil with 250 ml. of normal ammonium acetate solution. The total potassium content of the soil was determined by boiling 20 g. with 100 ml. conc. HCl and 5 ml. nitric acid for 2 hr. pH values were determined electrometrically on water extracts of the soil samples with the aid of a quinhydrone electrode.

RESULTS

Fig. 1 shows the distribution of exchangeable and water-soluble potassium in the soil before and during the course of the fertilizer
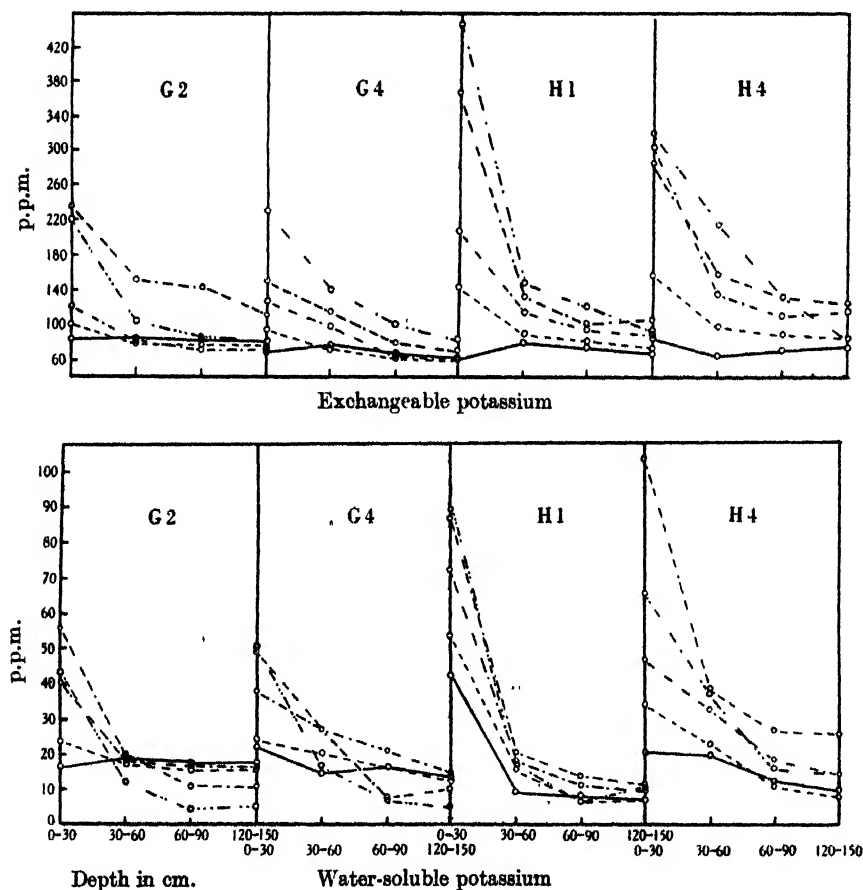

Fig. 1.

——————— Before the experiment.   – – – – – After first fertilization.
—·—·— After second fertilization.   —·—·—· After third fertilization.
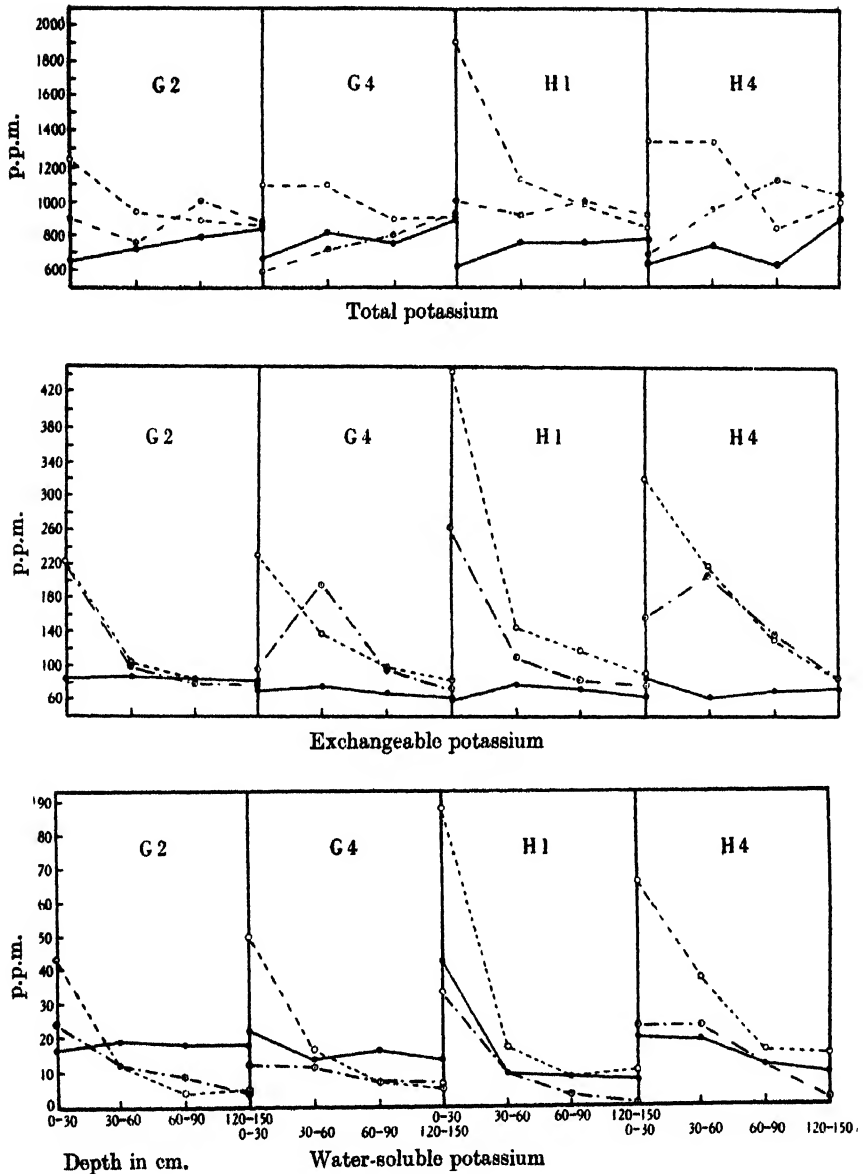·····—··· After fourth fertilization.

Fig. 2.

——————— Before the experiment.   – – – – After last fertilization.
                    ·——·——· After last irrigation.

experiment; Fig. 2 the distribution of total, exchangeable, and water-soluble potassium at the beginning and end of the fertilizer experiment and at the end of the irrigation experiment. The main points brought out by these diagrams are as follows.

1. Before application of fertilizer the potassium content of a red sandy clay was found to be distributed as follows: non-exchangeable and therefore slowly available potassium, 81–92 %; soluble and exchangeable potassium, 8–19 %.

2. When potassium sulphate is applied to this soil in four portions at a rate of 1800 g. per 9 sq. m., or when double this rate is used, the largest part of applied fertilizer is retained in the upper soil layer (0–30 cm.).

3. Potassium introduced into the soil by fertilizer treatment was distributed to a depth of 60 cm. in the following proportion: non-exchangeable potassium, 60–94 %; soluble and exchangeable potassium, 6–40 %.

4. There is a direct relationship between the amount of potassium applied and the amount of potassium retained by the soil. When the fertilizer ration applied is doubled (H1, H4) the amount of total, exchangeable, and soluble potassium retained in the upper soil layer (0–30 cm.) is somewhat more than double and also the amount of potassium retained in the second soil layer (30–60 cm.) is substantially increased.

5. By irrigating with double (G4, H4) instead of the normal (G2, H1) ration of water the concentration of total, soluble, and exchangeable potassium in the second soil layer (30–60 cm.) is increased.

6. When irrigation is not carried out in summer, soluble potassium ascends from the deeper layers to the upper soil layer (0–30 cm.); in winter, an opposite movement occurs and there is a loss of soluble potassium which decreases with increasing depth.

7. Successive summer irrigations with 1 or 2 cu.m. of water per irrigation lead to considerable losses of total, soluble, and exchangeable potassium from the soil by leaching.

8. A direct relationship between the rate of loss of total, exchangeable, and soluble potassium from the soil by leaching and the amount of water applied in irrigation exists only in plots which have received a normal fertilizer ration.

The effect of potassium fertilizer on the soil pH is slight. In the upper layer (0–30 cm.) there is after fertilization a slight movement towards the side of increased alkalinity, and in deeper layers a slight movement towards greater acidity. With double the normal ration of fertilizer the effect on soil pH was more marked. On repeated irrigation, soil pH changes due to fertilizer application are nullified.

THE COMPARATIVE DIGESTIVE POWERS OF ZEBU AND HIGH-GRADE EUROPEAN CATTLE

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THE problem of developing high-producing cattle in the tropics has claimed the attention of many workers. Existing types of local cattle are too slow maturing and insufficiently productive (especially as dairy animals) for European settlers, and efforts have, therefore, been made to get more economical stock by crossing local cows with bulls of recognized European breeds. This policy has resulted in half-bred animals which are superior to their dams, but subsequent top-crossing with European sires has not continued this improvement. Instead, as the progeny of half-bred cows are graded nearer to the European breed, an increasing number of constitutional failures occurs and many animals possessing too high an admixture of European blood in their ancestry are inferior economically to the unimproved native stock.

Efforts are now being made in many countries to determine what environmental or genetical factors are responsible for this failure of high-grade stock. Nutrition is one of the factors considered as possibly contributing to this unsatisfactory condition, but it is not the only factor involved for previous work (French, 1937) has shown, as had already been demonstrated by Carneiro & Rhoad (1936), that the retardation of growth in young high-grade stock is caused by factors other than nutrition. A number of publications, however, indicate that the nutritional standards for European cattle are not suitable for zebus and suggest that there are differences in the digestive powers of the two types.

Differences in the powers of extracting nutrients from food are mentioned chiefly by writers on the Indian zebu. Matson (1928-9) pointed out that European milk breeds have been bred for "characters which assist the effective use of the largest quantity of food", whereas the Indian zebus are able to make the "most efficient use of the smallest quantity of food". He also stated that "The European ox extracting 60 % from 30 lb. dry matter is inferior *in India* to the Indian ox which can only digest 20 lb. dry matter but extracts 75 %". Warth & Gossip (1930) found that their zebus gained in weight when the ration supplied only bare maintenance requirements if judged by European standards.

Also, Sayer (1934) concluded that European feeding equivalents were unsuited to Indian cows and that the latter had "a different digestive capacity". Warth (1927-8) considered the Indian zebus had higher digestive powers because they gave digestibility coefficients for rice straw which were higher than the corresponding American figures, but, as Carbery *et al.* (1934) realized later, American digestibility values could not be used in Indian digestion experiments.

No direct comparison of the digestibility powers of zebu and grade European cattle has been made by these workers, and there are no quantitative data to show whether the failure of European rationing standards is due to (*a*) differences in the digestive efficiencies of the two breeds, (*b*) incomplete knowledge of the compositions and feeding values of Indian foodstuffs, (*c*) differences in the powers of assimilating digested nutrients, or (*d*) the zebus having different nutritional requirements. Because of this, the following work attempts the direct comparison of the powers of digestion, without recourse to outside figures.

<div align="center">EXPERIMENTAL</div>

In the following work pure zebu and grade zebu × Ayrshire oxen were used. The animals were all healthy and had been fed and managed from birth under similar conditions. Two zebu and two grade Ayrshire oxen of the same ages were used in each digestibility trial, whilst three groups of zebu and grade oxen were employed to avoid errors due to individual peculiarities. The ages of the oxen varied from 14 to 39 months in the different trials, the foodstuffs examined ranged from coarse fibrous fodders to concentrates of low fibre content, and the rations fed differed considerably in protein content. With each group of animals, trials were made to see if there were any differences in the powers of digesting fodders and concentrates.

The compositions of the ten foodstuffs used in these trials are shown in Table I. These figures show the rather low protein but highly fibrous nature of the hays used, and are typical of East African hay from mixed grass species. The sample of maize meal had a slightly lower protein value than normal, but the other foodstuff analyses are well within the normal range for this territory.

Since the foodstuffs chosen for this series of trials provide a considerable range of variations for each food constituent examined, they should allow any differences in the digestive powers of zebu and grade European cattle to become apparent.

Table I. *Compositions of the foodstuffs (dry-matter basis)*

Trial no.	Foodstuff	Crude protein	Ether extract	Crude fibre	N-free extract	Total ash
1	Hay	7·54	1·45	35·57	44·01	11·40
2	Cottonseed	20·31	15·25	32·14	26·95	5·35
3	Hay	10·63	1·30	34·51	43·69	9·87
4	Concentrate mixture	22·90	13·29	18·51	40·00	5·30
5	Green grass	8·05	1·82	34·76	43·39	11·98
6	Hay	7·05	1·66	36·46	45·21	9·62
7	Wheat bran	14·90	2·70	12·28	66·15	3·97
8	Maize meal	8·92	1·79	3·18	83·59	2·52
9	Maize stalks	4·99	1·11	34·69	52·50	6·71
10	Hay	6·31	1·43	36·00	46·59	9·67

Part 1

The first trial was made on calves, one year old, fed an *ad lib.* ration of hay. All four animals consumed roughly the same amount and the faeces were collected over a 10-day period. The results, summarized in Table II, indicate that the zebu calves showed slightly higher digestibility coefficients for each food constituent examined.

The ration was then changed by feeding, each morning, just enough cottonseed to get complete consumption regularly in one feed, and in the trials 1 kg./day was fed to each animal. The cottonseed was fed whole with some of its lint still adhering to the seeds. In this trial the fibre content of the ration was maintained at a high level, and the results of the 10-day collecting periods are given in Table II.

Again the zebus showed slightly higher digestibility coefficients for each food component, but in this case the digestibilities recorded for the protein, fibre and ether extract constituents with the grade calves overlapped the range recorded for the zebus.

The differences between the average values for zebus and grades with these two pairs of young animals are not large, and though they may indicate a slight superiority in favour of the zebus, it is very doubtful if this would be of practical significance.

Part 2

Another pair of animals was used in the next two trials; they were older—19 months—and the grades were 60 lb. heavier. They were fed, in their first trial, an *ad lib.* ration of chaffed hay and the results obtained are given in Table II. Again it was found that the zebus gave slightly higher digestibility coefficients for all the components examined; the difference between zebus and grades being of the same order as for the previous group of animals.

After a period of rest, during which they were changed to a ration of

hay and a mixture of concentrates, a second trial was made with these animals. The concentrate mixture was composed of 1 kg. cottonseed, 0·4 kg. maize meal, and 0·4 kg. sesame cake daily, and was designed to contain almost half the proportional amount of fibre, a smaller percentage of oil, and 50 % more N-free extractives than the cottonseed fed to the younger calves. As before, a 10-day collecting period was carried through and the results are shown in Table II. In this trial there is practically no difference between the average digestibility coefficients for the zebu and grade calves, for whilst the zebus gave slightly higher figures for certain food constituents the grades gave higher values for the others.

Part 3

To see whether zebus always show the above-noted superiority in their powers of digesting fibrous fodder, a third group of animals was trained to the metabolism crates, and were fed an *ad lib.* ration of green *Cynodon plectostachyum* grass. When the 10-day collecting period commenced the grass was 2 ft. high and in all stages of maturity from flowering to the ripening of seed; the stems were becoming hard and leaves were drying off in some cases. Reference to Table I shows that the composition of this grass corresponds very closely to those of the hays used in Parts 1 and 2. The results of this trial, shown in Table II, indicate that, although the animals were of almost the same age as those in Part 2, there is no difference between the average digestibility coefficients found for the zebu and the grade oxen.

These animals were then changed to an *ad lib.* ration of hay made from a mixture of grasses and a further trial taken two months later, when the oxen were 21 months old. These results, given in Table II, show no differences in the digestive abilities of the zebu and grade oxen.

To test the digestibilities of these animals on a foodstuff of medium fibre and low-medium protein contents, wheat bran was fed at the rate of 1 kg./day. The results of this trial are summarized in Table II, where it is seen that much greater variations in the digestibility coefficients were found between the individuals of each pair of animals. The average values for the digestibilities of the ether extract and crude fibre fractions do not correspond for the two types of oxen, and are probably affected by the method of determination so that the direct comparison of the digestive powers is less easy. The coefficients for the total organic matter, however, correspond more closely and the general conclusion would be that the two types of oxen digested the wheat bran equally well.

A further trial was then carried out, using maize meal (fed at the rate of 1 kg./day) as representative of concentrates of low fibre and protein contents. The results obtained in this trial, when the oxen were 30 months old, are given in Table II. Though there was little difference between the average digestibility coefficients for the zebu and grade oxen, the grades gave the higher values for the total organic matter.

When these oxen were 33 months old a further trial was made on dried maize stalks after the ripe cobs had been removed. This is one of the common supplementary foodstuffs of the dry season in this territory, and in this trial chaffed stalks were fed *ad lib.* each morning whilst chaffed hay was fed *ad lib.* every afternoon. The figures obtained are shown in Table II. As was found with the green grass and hay examined earlier, neither type of ox showed higher values for every food component, but the average values for the organic matter were the same for both zebu and grade oxen.

Later, when these animals had reached 39 months of age, they were again used to record the digestibility of another sample of hay. The results of this trial are shown in Table II. In this trial the grade oxen showed slightly higher digestibility coefficients than the zebus in all the constituents examined, though the difference in the digestibilities of the organic matter is less than those recorded in favour of the zebus in Parts 1 and 2. Again the difference between the two types of oxen is not of practical significance.

DISCUSSION

In Table II the average digestibility coefficients for the zebu and grade European oxen are tabulated for easy reference.

The results indicate a slight superiority in the digestive powers of yearling zebu oxen for typical samples of hay and cottonseed. A slightly older group of animals (19 months) again showed that the zebu pair digested hay slightly more efficiently than their zebu × Ayrshire neighbours, but that a concentrate mixture was digested equally efficiently by both types. A third group of animals was then used to study a number of foodstuffs whilst the ages of the oxen changed from 18 to 39 months. With this group no differences in the average digestibility values were found between the two types of oxen for a sample of hay, green grass, chaffed maize stalks, and wheat bran, but the grade oxen gave slightly higher coefficients for the digestibility of another hay sample and for maize meal.

It is well known that individuals of the same breed of cattle give

Table II. *Digestibility coefficients obtained with zebu and grade Ayrshire cattle*

Foodstuff	Age in months	Type of animal		Dry matter	Organic matter	Crude protein	Ether extract	Crude fibre	N-free extract	Ash
Chaffed hay	12	Zebu	No. 10	59·12	61·10	60·62	47·66	67·16	56·38	43·74
			No. 14	58·24	59·80	57·13	48·43	65·98	55·55	45·56
			Average	58·68	60·45	58·87	48·05	66·57	55·97	44·65
	12	⅞ grade	No. 297	55·21	57·12	49·44	45·07	61·42	55·37	40·31
		¾ grade	No. 300	53·47	54·69	50·19	44·30	59·86	51·64	43·95
			Average	54·34	55·91	49·82	44·69	60·64	53·51	42·13
Cottonseed	15	Zebu	No. 10	67·14	67·17	66·92	88·95	55·35	69·12	66·73
			No. 14	61·26	62·58	63·69	89·67	46·61	65·46	37·81
			Average	64·20	64·88	65·31	89·31	50·98	67·29	52·27
	15	⅞ grade	No. 297	58·30	60·56	64·88	91·93	49·46	52·79	18·30
		¾ grade	No. 300	57·91	59·97	64·24	86·25	43·25	61·82	21·48
			Average	58·11	60·27	64·56	89·09	46·36	57·31	19·89
Chaffed hay	19	Zebu	No. M1	45·84	50·66	47·35	51·04	62·66	41·90	——
			No. M2	46·40	51·53	46·42	52·59	61·64	44·84	—
			Average	46·12	51·10	46·89	51·82	62·15	43·37	—
	19	¾ grade	No. 272	41·42	46·86	45·32	33·75	58·23	38·82	—
		¾ grade	No. 274	41·45	47·09	40·89	35·40	58·26	40·27	—
			Average	41·44	46·15	43·11	34·58	58·25	39·55	—
Concentrate mixture	21	Zebu	No. M1	71·17	72·20	76·04	87·04	61·86	69·86	52·65
			No. M2	69·90	71·15	72·17	90·30	61·37	68·73	47·54
			Average	70·54	71·68	74·11	88·67	61·62	69·30	50·10
	21	¾ grade	No. 272	71·55	71·63	76·57	85·17	63·27	66·47	70·02
		¾ grade	No. 274	70·81	70·79	79·88	86·67	62·81	64·04	75·11
			Average	71·18	71·21	78·22	85·92	63·04	65·25	72·56
Green grass	18	Zebu	No. 1	44·85	48·56	49·03	69·24	52·62	44·25	16·79
			No. 2	45·41	49·13	52·15	72·79	52·78	44·68	18·08
			Average	45·13	48·85	50·59	71·02	52·70	44·47	17·44
	18	¾ grade	No. 305	46·36	50·34	50·79	53·68	53·26	47·80	16·95
		⅞ grade	No. 298	44·68	48·34	47·51	49·21	52·63	45·05	17·67
			Average	45·52	49·34	49·15	51·45	52·95	46·43	17·31
Chaffed hay	20	Zebu	No. 1	44·60	47·23	39·87	47·69	54·39	42·54	19·33
			No. 2	45·38	48·05	40·82	33·06	54·72	44·36	20·25
			Average	44·99	47·64	40·35	40·37	54·55	43·45	19·79
	20	¾ grade	No. 305	44·84	47·95	41·16	46·80	53·01	44·98	15·59
		⅞ grade	No. 298	44·79	47·16	36·16	46·05	52·11	44·88	22·82
			Average	44·82	47·56	38·66	46·43	52·56	44·93	19·21
Wheat bran	25	Zebu	No. 1	59·13	61·46	71·21	51·07	13·50	68·59	2·77
			No. 2	58·59	63·36	70·00	68·89	15·66	70·49	—
			Average	58·86	62·41	70·61	59·98	14·58	69·54	1·38
	25	¾ grade	No. 305	57·24	58·73	63·55	34·32	23·36	65·21	21·30
		⅞ grade	No. 298	62·61	65·23	70·71	16·58	44·75	69·78	——
			Average	59·93	61·98	67·13	25·45	34·05	67·50	10·65
Maize meal	30	Zebu	No. 1	82·19	78·04	77·99	71·70	73·66	84·91	24·87
			No. 2	82·40	83·70	73·67	71·70	74·11	85·39	31·89
			Average	82·30	80·87	75·83	71·70	73·89	85·15	28·38
	30	¾ grade	No. 305	82·95	84·26	72·97	75·19	70·55	86·18	32·33
		⅞ grade	No. 298	86·37	88·44	80·61	66·47	57·89	90·92	6·00
			Average	84·66	86·35	76·79	70·33	64·22	88·55	19·16
Maize stalks	33	Zebu	No. 1	66·91	67·51	53·41	75·21	72·49	65·45	58·58
			No. 2	63·92	65·87	45·19	66·16	69·11	65·71	36·99
			Average	65·42	66·69	49·30	70·68	70·80	65·58	47·78
	33	¾ grade	No. 305	65·51	66·71	30·99	56·65	80·31	61·33	48·82
		⅞ grade	No. 298	64·79	67·25	37·65	64·10	80·22	61·95	31·20
			Average	65·15	66·98	34·32	60·37	80·27	61·64	40·01
Chaffed hay	39	Zebu	No. 1	59·64	60·00	46·20	51·11	68·29	55·63	51·06
			No. 2	58·84	59·06	43·81	50·53	69·01	53·71	53·92
			Average	59·24	59·53	45·01	50·82	68·65	54·67	52·74
	39	¾ grade	No. 305	61·96	61·93	49·97	58·81	71·97	55·89	62·60
		⅞ grade	No. 298	60·78	60·50	48·07	57·21	70·12	55·32	61·76
			Average	61·37	61·22	49·02	58·01	71·04	55·60	62·18

slightly different digestibility coefficients for any given foodstuff, and also that any given animal may give slightly varying values at different times. The method of determining digestibility by subtracting the faecal excretion from the intake, suffers from a number of disadvantages and it is recognized that the digestibility coefficients, obtained by this method with a given group of animals, are not absolute values but convenient practical guides. A certain amount of flexibility must always be attached to digestibility coefficients and small differences between the average values for the zebu and grade European cattle cannot be considered significant. If we examine the average figures for organic matter in Table II we see that the percentage digestibilities of the organic matters by the two types of oxen differed by less than 0·5 in five of the ten foodstuffs examined, whilst the maximum difference of only 5·5 was recorded in favour of grade oxen for maize meal. From these results it is claimed that zebu oxen do not possess significantly superior digestive powers over grade zebu × Ayrshire oxen, nor with coarse fodders do they always show a slightly higher digestive efficiency.

Table III. *Digestible nutrients and feeding values recorded with zebu and grade Ayrshire cattle*

Foodstuff	Type of animal	Age in months	Digestible protein	Digestible ether extract	Digestible N-free extract	Digestible crude fibre	Starch equivalent
Hay	Zebu	12	4·44	0·71	24·63	23·68	32·21
	Grade		3·76	0·66	23·55	21·57	29·47
Cottonseed	Zebu	15	13·26	13·62	18·13	16·38	68·60
	Grade		13·11	13·59	15·45	14·90	64·51
Hay	Zebu	19	4·98	0·67	18·95	21·45	26·94
	Grade		4·58	0·45	17·28	20·10	22·54
Concentrate mixture	Zebu	21	16·97	11·78	27·72	11·40	80·00
	Grade		17·91	11·42	24·74	10·62	78·73
Green grass	Zebu	18	4·07	1·29	19·30	18·32	23·74
	Grade		3·96	0·94	20·15	18·41	23·92
Hay	Zebu	20	.2·84	0·67	19·64	19·87	22·33
	Grade		2·73	0·79	20·31	19·16	22·36
Wheat bran	Zebu	25	10·52	1·62	46·00	1·79	48·00
	Grade		10·00	0·69	44·65	4·18	47·04
Maize meal	Zebu	30	6·76	1·28	71·18	2·35	82·32
	Grade		6·85	1·26	74·02	2·04	84·91
Maize stalks	Zebu	33	2·46	0·78	34·43	24·56	42·67
	Grade		1·71	0·67	32·36	27·85	42·98
Hay	Zebu	39	2·84	0·73	25·47	24·71	33·36
	Grade		3·09	0·83	25·90	25·57	35·08

If the digestible nutrients and the feeding values of the foodstuffs are calculated by Kellner's methods from the above tables the data in Table III are obtained, from which it is seen that for all practical rationing

purposes the starch equivalent and digestible protein values are not significantly different for the two types of oxen.

It is also interesting to observe that, though both 3/4 and 7/8 grade Ayrshire cattle were used in the above work, there was no indication that higher grading affected the digestibility coefficients or feeding values.

SUMMARY

1. With three different groups, each of two zebu and two zebu × Ayrshire grade oxen, and ten typical East African feeding stuffs, no significant difference was found between the average digestibility coefficients recorded with the zebu and the grade oxen.

2. The slight differences in feeding values were also of no practical significance.

3. Some of the zebu × Ayrshire cattle were 3/4 and others 7/8 Ayrshire but the higher grading to the European breed apparently did not affect the digestive powers.

REFERENCES

CARBERY, M., CHATTERJEE, I. & HYE, M. A. (1934). *Ind. J. Vet. Sci. Anim. Husb.* **4**, 295.

CARNEIRO, G. G. & RHOAD, A. O. (1936). *Trop. Agric.* **13**, 177.

FRENCH, M. H. (1937). *Ann. Rep. Dep. Vet. Sci. Tanganyika*, p. 65.

MATSON, J. (1928-9). *J. Cent. Bur. Anim. Husb. Dairying, India*, **2**, 83.

SAYER, W. (1934). *Agric. and Livestock, India*, **4**, 105.

WARTH, F. J. (1927-8). *J. Cent. Bur. Anim. Husb. Dairying, India*, **1**, 122.

WARTH, F. J. & GOSSIP, F. J. (1930). *Mem. Dep. Agric. India*, **10**, 1.

GROWTH AND DEVELOPMENT IN THE PIG, WITH SPECIAL REFERENCE TO CARCASS QUALITY CHARACTERS

PART III. EFFECT OF THE PLANE OF NUTRITION ON THE FORM AND COMPOSITION OF THE BACON PIG

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(With Plates 17–30 and Four Text-figures)

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PART III. EFFECT OF THE PLANE OF NUTRITION ON THE FORM AND COMPOSITION OF THE BACON PIG

(1) LIVE-WEIGHT GROWTH CURVES

THE individual live-weight growth curves of the four pigs in each set are shown in Text-fig. 28 (castrate males) and in Text-fig. 29 (females).[1] Reading across, each set comprises one animal on each of the four treatments—High-High, Low-Low, High-Low, and Low-High. The curves have been constructed from the weekly live weights (see Appendix IV).

[1] This is a continuation of work published in the previous number of the *Journal*: it is hoped to publish a concluding part in the next number of the *Journal*. A list of references and Appendix IV will be given at the end of the concluding part.

Since treatment differences in this experiment lie essentially in differences in the shape of the growth curve, the differences within the same type of curve, as well as the order of the difference between the types, are of considerable importance. It will be seen later that much of
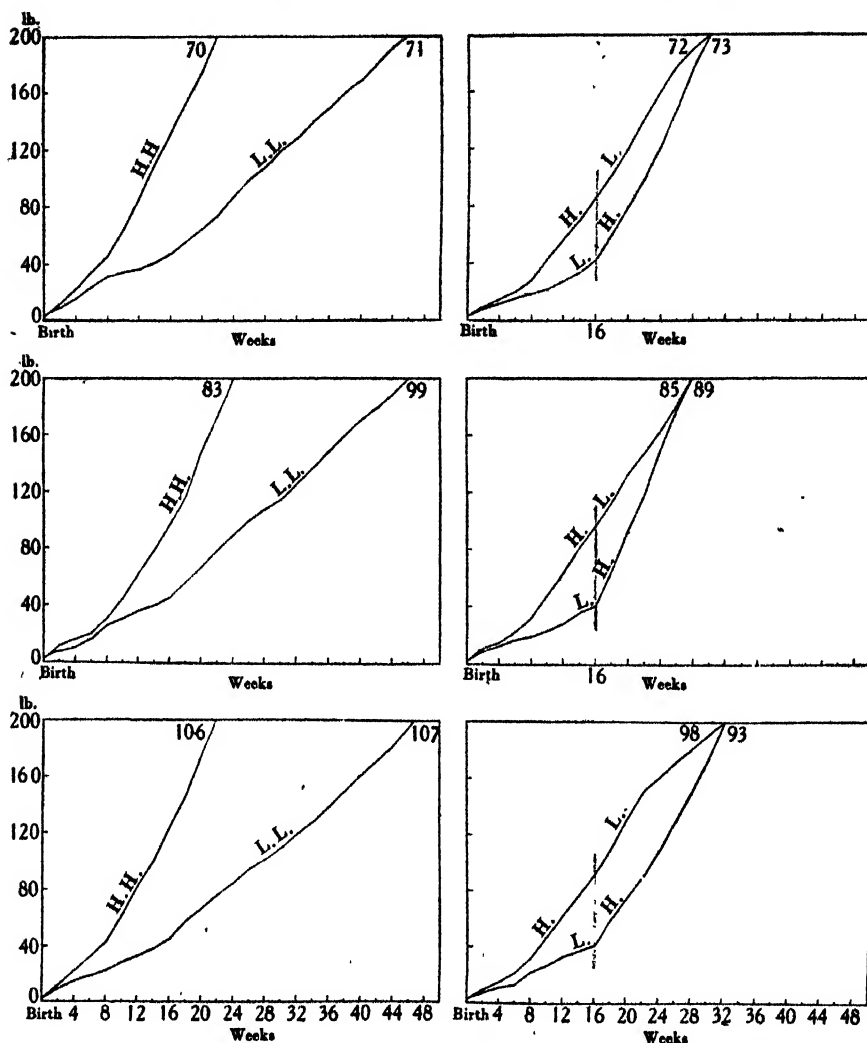
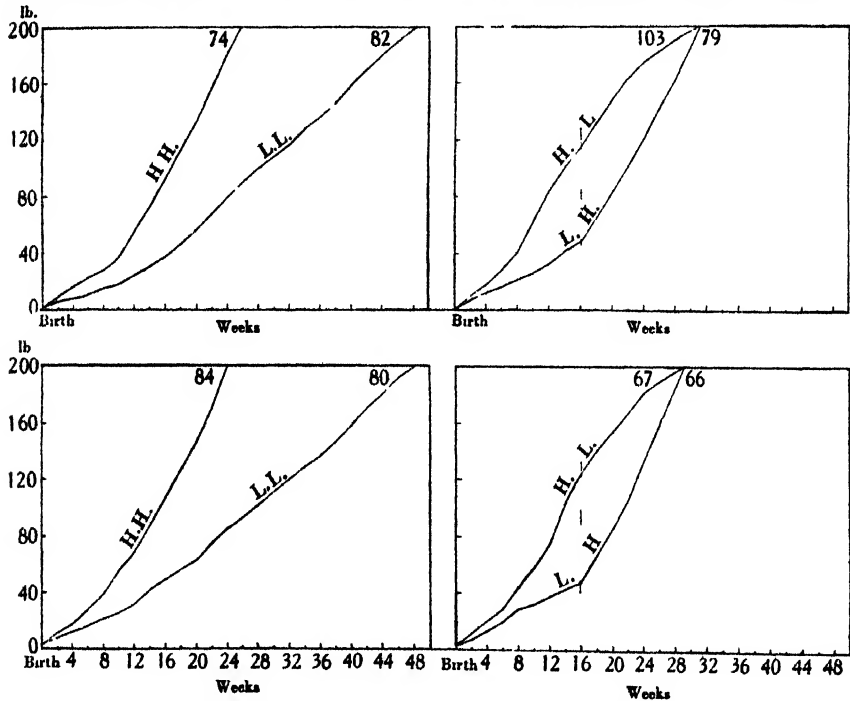Text-fig. 28. Individual live-weight growth curves—High protein 200 lb. series. (Males.)

what variation is present in composition of the animals on the same treatment is capable of explanation on a basis of differences in the shape of the individual growth curves.

In the two extreme treatments, the High-High and Low-Low, the pigs on a High Plane from birth reached 200 lb. at an average age of

165 days as against the 180 days planned as a minimum (see Text-fig. 1). One pig only—pig 74—required the full period, while pigs 70 and 106 needed only 154 and 155 days respectively. Those requiring the longer period were characterized by poorer growth during the early stages, the reasons for which have been described in Part II. Animals on a Low Plane of nutrition from birth were controlled so as to reach weight in 327 days, thus exceeding the minimal age by 27 days. Variations within these—

Text-fig. 29. Individual live-weight growth curves—High protein 200 lb. series. (Females.)

from 315 to 339 days—were not accidental but due to an effort to maintain a similar growth curve difference between the High-High and the Low-Low pairs within each set. From the weight of the former round about 16 weeks, their approximate age at 200 lb. live weight was forecast, and the rate of the growth of the Low-Low counterpart modified accordingly. Thus pig 82 had to be slowed down slightly as compared with the other Low-Lows, since High-High pig 74 was not making the same growth as others on the same treatment. At the other extreme, pig 71 was allowed to grow somewhat faster than the others for the High-High animal of the same set—pig 70 was growing at an extremely rapid rate.

   In the other two treatments, where the individuals of each High-Low

and Low-High pair had to reach 200 lb. live weight on the same day, control was effected through the High-Low member. By relation to its own live weight and that of its Low-High counterpart at the same time, its ration was adjusted throughout the period, so that the two curves finally converged. As rapid a rate as possible was required from the Low-High pigs after 16 weeks. This was effected by a quick change from the restricted to an *ad lib.* ration; the period requiring about 3 days. The resulting rapid growth of the Low-High animals is responsible for the difference in the form of the curves from the theoretical, for these two treatments, and for the reduction in the expected average age of 240 days (Text-fig. 1) to 211 days at 200 lb. In controlling the rate of growth of the High-Low pigs, an accentuation of the decrease in rate was aimed at during the later stages. This, however, was found difficult in all cases, due to the rapid growth of the Low-Highs and impossible in one case (pair 85 and 89) as a result of a combination of an extremely high growth rate of the Low-High animal and a relatively low weight in the High-Low at 16 weeks.

While we have made no special study of the point, it will be observed that the curves of the Low-High pigs do not exhibit a more rapid rate than a normal animal makes at any period in its life as reported by Thompson & Mendel (1917) for rats subjected to re-feeding after a period of retardation. The gains per week of our Low-High pigs tended to be higher than those expected from normally fed animals, but were no higher than those of our pigs on a High Plane throughout the feeding period. Much of the initial increase in live weight shown after the 16-week period is undoubtedly due to stomach contents. The marked change in ration—from 1 to 5 lb. of meal in less than a week, with a double ration of separated milk—produced a "pot-bellied" appearance in the pigs. This effect persisted for some time, and it is our impression that in reality a lag in the rate of increase in "empty live weight" occurred which is not evident from the curves.

Details of the food consumption of the pigs on the four treatments are given in Appendix IV.[1]

In the subsequent presentation of the results, three main methods are employed. Mean figures for each treatment—based on the mean of males and females in each case—and the proportionate effect taking the Low-Low treatment as a base are presented for all the characters studied. For the major characters, the significance of the differences noted are tested by Fisher's (1934) analysis of variance, which will also be employed

[1] This will be given at the end of the concluding part in the next number of the *Journal*.

for detailed parts where the nature of the treatment effect follows a different trend from that of the great bulk of characters. Relative effect upon body and carcass proportions, and upon the major bone groups are also studied photographically. Raw data are given in Appendix IV.

In considering the results it will be recognized that as between the High-High and Low-Low treatments we are dealing with a clear-cut difference in the plane of nutrition operative from birth, but differing from our 16-week study in that the animals are of the *same* final body weight but of *different* age. A similar comparison is available as between the High-High and High-Low pigs over a shorter time interval and from a common base-line attained by *good* nutrition for the first 16 weeks of life. A third comparison of similar type exists as between the Low-High and Low-Low, but in this case from a common base-line attained by relatively *poor* nutrition for the first 16 weeks. Differing from these three is the comparison afforded by the High-Low and Low-High treatments where we have pigs of the *same age* and the *same body weight* but with differently shaped growth curves produced by reversal of the level of nutrition for approximately half of the total feeding period. These four comparisons provide the more convenient basis for discussing the nature of the relative effects. At the same time, the other two possible comparisons must not be deemed unimportant—High-High with Low-High, and High-Low with Low-Low. These are of definite practical and theoretical importance and receive equal consideration.

(2) Effect on body proportions

The relative effects of the four treatments upon the live form are shown in Pl. 17 (castrate males and females). These have been prepared as described in Part II, the pigs being scaled to the same shoulder-trotter height. Colour differences in these and other photographs are due to variable lighting conditions consequent on the incidence of fog on many occasions.

Though the attainment of the same body weight has tended to reduce the extent of differences noticed as between High and Low Plane animals at 16 weeks, these are essentially similar. Thus in the High-High animals, the head, neck and legs are relatively short as compared with the Low-Low, but the late-developing parts—body depth, loin and hams—are relatively better developed. Similar differences are apparent as between the High-High and High-Low, where the lower level of nutrition during the later stages of growth in the latter has tended to produce pigs similar in form,

though not to such an extreme degree, to the Low-Low animals. It would appear that full development of the later developing regions has been retarded by the imposition of inadequate nutrition, though growth has continued in the earlier developing fore-end of the body.

The effects upon the proportions of the Low-High pigs are extremely interesting; here we find that even to a greater degree than in the High-High, there has been a greater relative development of the hind- as compared with the fore-end of the body. The legs are extremely short, the body deep and the hams and loin well filled. The head is relatively small and the neck short and thick. Remembering that at 16 weeks (Part II) the late-developing parts were the most severely restricted by under-nutrition in these pigs, it would appear that the change to a high level of feeding has exerted a marked differential effect in favour of these parts initially penalized.

The difference between the sexes might be noted. In all treatments the females appear to carry less "condition" than the castrate males on the corresponding treatment. Differences between treatments follow the same trend in both sexes. This difference between hogs and gilts is responsible for the difference in body form of pig. 93 in Pl. 17 which does not show the same degree of plumpness as the males on the same treatment. Although sex is thus against the comparison, she shows the same type of difference from her High-Low counterpart pig 98 as is shown between the other High-Low and Low-High pairs.

The carcass form of the pigs is shown in Pl. 18 (castrate males) and Pl. 19 (females), the treatment sets in this case reading across instead of down, with the carcasses scaled to the same body length.

It will be observed that relative effects noted above are borne out in this view also. The Low-Low animals have the relatively longest heads and legs, and the poorest hams. The loin is narrow and gives the impression of poor development. The High-Low pigs approach them most, showing similar effects. The animals finishing on a high plane of nutrition have the shortest legs and the best developed hind-ends, well-filled hams and loin with the balance in favour of the Low-High animals. The relative difference in the breadth of body is probably the outstanding feature. In all cases the pigs poorly fed during the later stages of growth show the narrowest carcasses with a greater effect upon those poorly fed throughout—the Low-Low. On the other hand, the High-Plane pigs are correspondingly wider throughout their length, with the Low-High treatment showing a slightly greater width. Sex differences similar to those above are also apparent here.

These visual differences in form are consistent in the main with the relative difference in the weight of the anatomical joints of the different regions (Table 37). Note that the heads are heaviest in the Low-Low pigs and lightest in the High-High, while the later developing loin region is lightest in the Low-Low and heaviest in the Low-High.

Table 37. *Effect of plane of nutrition on body proportions at 200 lb.*

	Mean weight (g.)				Proportion			
Part of body	High-High	High-Low	Low-High	Low-Low	High-High	High-Low	Low-High	Low Low
Head	4901	5054	4902	5589	87·6	90·4	87·7	100
Neck	5856	6743	6573	6267	93·4	107·5	104·9	100
Shoulders (2)	11023	11354	10728	11305	97·5	100·4	94·8	100
Thorax	18330	17226	18454	16272	112·6	105·8	113·4	100
Loin	6090	6335	7107	5445	111·8	116·3	130·5	100
Legs (2)	12530	13807	12088	13406	93·4	102·9	90·1	100
Pelvis	6083	5730	5832	5642	107·8	101·5	103·3	100

Viewed broadly, it will be recognized that two distinct types of animal have been produced from the four treatments; the High-High and Low-High have resulted in like animals as have also the Low-Low and the High-Low. The two types show marked differences, and these are such as would be expected from our observations on the effect of varying planes of nutrition on the relative growth of early- and late-developing regions of the body (see Part II). The High-High and Low-High pigs closely approached the body form of an early-developing breed like the Middle White, while the High-Low and Low-Low were characteristic of an extreme late-developing type breed. The differences between the two pairs of treatments producing a "like" result are also in line with this situation, i.e. the provision of ample nutrition following a period of retarded growth in the case of the Low-High pigs has tended to encourage most those parts of the body which are normally making a greater amount of growth later in life (see Age Series, Part I). We will later see how far this approach provides an adequate explanation of the facts.

(3) Effect upon carcass composition

From both theoretical and practical points of view, perhaps the greatest interest in this experiment centres round the absolute and relative effects of the treatments on the composition of the carcass. How far it is possible to control the bone, muscle and fat complex has been the major problem to which we have sought an answer.

That a considerable effect has been produced on each of these tissues

Table 38. *Effect of plane of nutrition on composition of carcass at 200 lb.*

Plane of nutrition	Mean weights (g.)				% carcass weight				Proportion, Low Plane = 100			
	High-High	High-Low	Low-High	Low-Low	High-High	High-Low	Low-High	Low-Low	High-High	High-Low	Low-High	Low-Low
Skeleton	7186	7525	6398	8014	10·98	11·23	9·67	12·39	89·7	93·9	79·8	100
Muscle	26362	30054	24038	31771	40·26	44·86	36·32	49·13	83·0	94·6	75·7	100
Fat:												
Subcutaneous	18443	16024	21422	12171	28·17	23·91	32·37	18·82	151·5	131·7	176·0	100
Intermuscular	6653	6332	7783	5614	10·16	9·45	11·76	8·68	116·7	112·7	138·6	100
Total	25096	22356	29205	17785	38·33	33·36	44·13	27·50	140·8	125·7	164·2	100
Skin	3453	3629	3207	3736	5·27	5·42	4·85	5·78	92·4	97·1	85·8	100
Tendon, glands, waste, etc.	2102	2556	2091	2717	3·21	3·81	3·16	4·20	77·4	94·0	76·9	100
Loss in dissection	1331	883	1232	640	2·03	1·32	1·86	1·00	—	—	—	—

can be observed from Table 38, which summarizes the mean results of the four treatments on an absolute, a percentage, and a proportional basis.

At the one extreme, the Low-Low pigs have the greatest amount of bone and muscle, and the least amount of fat. At the other, the Low-High animals have the least bone and muscle, and the most fat. Intermediate
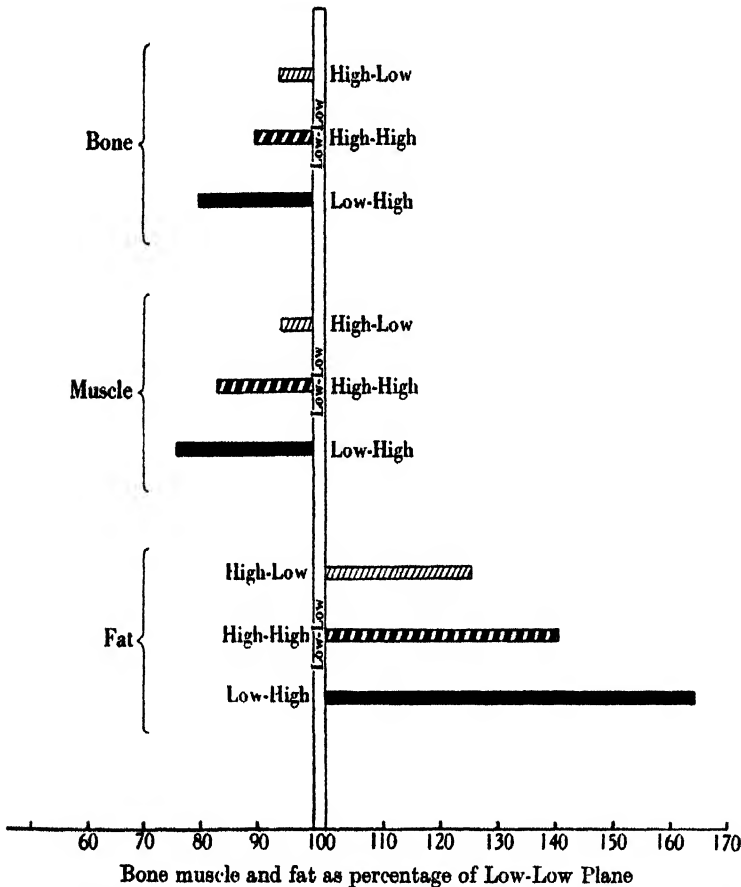
Text-fig. 30. Effect of plane of nutrition on relative composition of carcass at 200 lb.

between these, the High-High pigs tend to approach in composition the Low-High but with more bone and muscle and less fat than the latter. The High-Low pigs, on the other hand, are nearer the Low-Low with but slightly less bone and muscle, though more fat. As between the High-Low and Low-High treatments, the difference is relatively large in all three tissues, with the former showing a greater amount of bone and muscle and the latter the greater quantity of fat.

The relative differences can be observed in the last column of Table 38

and in Text-fig. 30, where the data are represented in histogram form. All treatments have been placed on a comparable basis by taking the Low-Low treatment as a "base-line" and expressing the weight of tissue in each case as a percentage of the weight of corresponding part of the latter. This permits a comparison of the relative effects, not only for the one tissue between treatments but also for the different tissues within each treatment. Note that by taking the Low-Low as a base, bone and muscle both become negative (relative to Low-Low as 100) and fat-positive for all three treatments, and that the order of treatment effect is the same for each tissue, i.e. Low-Low, High-Low, High-High and Low-High. Relative effect increases in this order in a negative direction for bone and muscle, and in a positive direction for fat.

Remembering that we are dealing with animals of the same body weight, and that accordingly the margin available for variation in the amount of the three tissues is limited, the extent of the differences produced is extremely high. In bone, the Low-High pigs have approximately 20%, the High-High 10%, and the High-Low 6% *less* than the Low-Low pigs. In muscle, similar figures are Low-High 25%, High-High 17%, and High-Low 5% *less*. In total carcass fat, the Low-High pigs have 64%, the High-High 41%, and the High-Low 26% *more* than the Low-Low. The relative effect upon the subcutaneous fat is even greater. The treatment yielding the fattest pigs—the Low-High—shows a 76% greater quantity than the treatment yielding the leanest animals—the Low-Low. The importance of these effects from the carcass quality angle receives additional emphasis from the data of Table 38a.

Table 38a. *Effect of plane of nutrition on proportions of bone, muscle and fat in carcass*

Ratio	High-High	High-Low	Low-High	Low-Low
Muscle/bone	3·67	3·99	3·76	3·96
Fat/bone	3·48	2·97	4·56	2·22
Fat/muscle	0·95	0·74	1·21	0·51

The relative effect upon skin, and upon tendon, glands and waste, follows a similar trend to that on bone and muscle; the treatments fall in the same order for these tissues, and in each case the effect is in a negative direction as compared with the Low-Low.

It might be mentioned at this stage that, though referring specifically to total bone, muscle, and fat, Text-fig. 30 also provides a fair picture of the relative effect upon these tissues in individual parts of the body. The order or general trend of effect *between* treatments is the same for

an individual bone or bone group as for the total skeleton; it is the same for fat in an individual joint as for total fat; for any particular muscle unit as for total muscle. Differences lie only in degree.

The statistical significance of the results for bone, muscle, and fat has been tested by analysis of variance. In Table 38 the data presented are based on the mean of the male and female means in each treatment. In the following data, the true treatment means are necessarily employed. Their absolute values relative to those of Table 38 are weighted by the preponderance of males in each treatment, but since the ratio is balanced -- three sets of hogs and two of gilts in each case---the relative position is unaffected. The one case of sex unbalance in the Low-High treatment fortunately occurs where it can exert no important effect upon the validity of the statistical comparisons made. This will be made clear during the subsequent examination of the data. Though sex differences are thus ignored -the numbers in each treatment are insufficient to permit statistical comparison of sex effects--its influence has been eliminated in part by isolating the variance between sets. A large part of the latter is likely to be due to sex.

Table 39. *Analysis of variance of total bone (g.)*

Variation	Degrees of freedom	Sum of squares	Mean square	
Between treatments	3	5938026	1979342	$Z = 1 \cdot 5970$ S.S.
Between sets	4	1784909	446227	$Z = 0 \cdot 8530$ N.S.
Error	12	972227	81019	
Total	19	8695162	—	

S.S. = significant at 1% point.　　　　N.S. = not significant.

The effect of the treatments upon bone (Table 39) is highly significant, the value of z being almost twice that necessary at the 1% point. The standard error per pig is 283·0 g. or 3·9% of the mean, a figure indicating an extremely satisfactory degree of experimental precision. The standard error of the treatment means is 126·6 g. The interrelations of the various treatments are presented in Table 40, from which any desired comparison can be readily observed. Several points might be noted here.

Except for one pair, all treatments differ significantly in their effect on total skeletal weight. In this pair—the High-High and High-Low— the difference falls just short of the level necessary for significance at the 5% point. While this is the case in respect to their bone weight difference, it will be shown later that this pair differs significantly at the 1% point in respect to bone form (see under Skeleton).

Table 40. *Table of significance—skeleton, muscle, fat and skin*

	High-High	High-Low	Low-High	Low-Low	High-High	High-Low	Low-High	Low-Low
		Skeleton				Muscle		
High-High	**7135**	N.S.	S.S.	S.S.	**26101**	S.S.	S.S.	S.S.
High-Low	N.S.	**7451**	S.S.	S.	S.S.	**29531**	S.S.	S.
Low-High	S.S.	S.S.	**6482·6**	S.S.	S.S.	S.S.	**24312**	S.S.
Low-Low	S.S.	S.	S.S.	**7988·8**	S.S.	S.	S.S.	**31773**
		Fat				Skin		
High-High	**25155**	N.S.	S.	S.S.	**3440**	N.S.	N.S.	N.S.
High-Low	N.S.	**22933**	S.S.	S.S.	N.S.	**3549**	S.	N.S.
Low-High	S.	S.S.	**28610**	S.S.	N.S.	S.	**3248**	S.S.
Low-Low	S.S.	S.S.	S.S.	**17923**	N.S.	N.S.	S.S.	**3687**

S.S. =significant at $P<0.01$.   S. =significant at $P<0.05$.   N.S. =not significant.
The mean is shown in heavy type.

In one case also, the Low-Low and High-Low, the difference in bone weight is sufficient for significance only at the 5% level. This pair is one of those to which attention has already been drawn as approaching each other both in body form and total composition.

In the four remaining comparisons, differences in weight of bone are significant at the 1% point. Between the heaviest (Low-Low) and lightest boned treatment (Low-High), the difference is 8·37 times the standard error of difference ($126·6\sqrt{2}$). Between the High-Low and Low-High (pigs of the same age and weight), the difference is highly significant at 5·44 times its standard error. Between the two extreme treatments — High-High and Low-Low—the difference is of the order 4·75 times, and between High-High and Low-High "t" is equal to 3·63. It will be noted that all three treatments have a significantly heavier skeleton than the pigs of the Low-High lot, despite the presence of a greater proportion of females in this treatment which is likely to have increased the mean weight of bone over its probable level if the normal sex ratio had existed. (Females are characterized by heavier bones than hogs— see under Sex differences.) Significance between all treatments and the Low-High is thus likely to be under-estimated rather than over-estimated.

Table 41. *Analysis of variance of muscle (g.)*

Variation	Degrees of freedom	Sum of squares	Mean square	
Between treatments	3	168,883,041·8	56,294,347·27	$Z=1·7797$ S.S.
Between sets	4	40,229,798·2	10,057,449·55	
Error	12	19,229,123·0	1,602,426·91	
Total	19	228,341,963·0	—	

S.S. =significant at 1% point.

Treatment effects upon total muscle are also strongly significant at the 1% point (Table 41). The standard error per pig is 1423·2 g. or 5·1% of the mean. The standard error of the treatment means is 566·1 g.

From Table 40 it will be observed that all six possible comparisons are significant; two pairs are significant only at the 5% point and the remainder at the 1% level. In respect to the former, these are the treatments approaching each other most closely in respect to other tissues also; the Low-Low with High-Low, and the High-High with Low-High.

Maximum difference exists between the same two treatments giving the largest effect upon skeletal weight; the Low-Low with Low-High, where the difference in favour of the former is 9·32 times its standard error. Between High-Low and Low-High the difference is also strongly significant with 6·51 times its standard error, while as between the two extreme treatments, High-High with Low-Low, the value is 7·08.

Though not differing significantly in bone weight, the High-Low pigs (which, of the pair, have the greater amount of bone) have significantly more muscle than the High-High, the difference being 4·28 times its standard error.

All treatments have produced animals with significantly more muscle than the Low-High treatment; as with bone, the higher female ratio of the latter will tend, however, to underestimate the difference, since gilts are characterized by more muscle than hog pigs.

The analysis of variance for total fat is given in Table 42. Here again Z is strongly significant at the 1% level. The standard error per pig is 2111·5 g. or 8·9% of the mean. The latter figure provides a measure of the relatively higher variability of this tissue as compared with bone and muscle, a result not unexpected in view of the relative immaturity of fat as compared with the latter tissues. The standard error of the treatment means is 944·3 g.

Table 42. *Analysis of variance of total fat (g.)*

Variation	Degrees of freedom	Sum of squares	Mean square	
Between treatments	3	300,872,068	100,290,689	$Z = 1·5566$ S.S.
Between sets	4	69,796,174	17,449,044	$Z = 0·6823$ N.S.
Error	12	53,505,482	4,458,790	
Total	19	424,173,724	—	

S.S. = significant at 1% point.   N.S. = not significant.

The differences between five of the six comparisons are significant (Table 40). Between the Low-Low and Low-High pigs the difference is 8·01 times its standard error; between the High-Low and Low-High

the value is 4·25 times; and between Low-Low and High-High, 5·42 times. All three are thus strongly significant at the 1% point.

The difference between Low-Low and High-Low is also significant at this level with 3·75 times its standard error. The other "like" pair, High-High and Low-High, similarly show a lower figure, and with a difference of 2·59 times its standard error, vary significantly only at the 5% point.

Only between the High-High and High-Low is the difference not large enough for significance. This is somewhat unexpected, as several practical pig-feeding trials have shown that restriction of food during the later stages of fattening reduces the amount of back fat (Murray *et al.*, 1933; Ellis & Zeller, 1934; Mansfield & Trehane, 1936; Mansfield *et al.*, 1937; Fishwick, 1936). The High-Low pigs definitely show this tendency to a marked degree in four pairs of pigs of the five involved. In one pair, however (pigs 83 and 85), the High-Low animal has more fat than the High-High (see Appendix IV). With the few total animals involved this is sufficient to disturb the statistical relationship. The situation is capable of explanation on a basis of the difference in the shape of the individual growth curves of the pigs concerned. Pig 83 had the slowest rate of growth of the High-High pigs, while pig 85 had the fastest rate of the High-Low. The latter could not be slowed down during the later stages owing to the rapid growth of its Low-High counterpart (pig 89) (see Text-fig. 28). The position, rather than detracting from, thus provides supplementary confirmation for our explanation of the relative treatment effects upon this tissue (see below).

In respect to total skin, the analysis of variance (Table 43) shows that the treatment effects are significant only at the 5% point. The standard error per pig is relatively small, amounting to 216·1 g. or 6·1% of the mean. The standard error of the treatment means is 96·7 g.

Table 43. *Analysis of variance of skin (g.)*

Variation	Degrees of freedom	Sum of squares	Mean square	
Between treatments	3	521,951	173,984	$Z = 0.6577$ S.
Between sets	4	1,094,165	273,541	
Error	12	560,412	46,701	
Total	19	2,176,528	—	

S. = significant at 5% point.

From Table 40 it will be observed that only two treatments differ significantly in the weight of skin: the Low-Low with Low-High, where

the difference in favour of the former amounts to 3·21 times its standard error and is significant at the 1% point; and the High-Low with Low-High, where the former is significantly heavier than the latter at the 5% point. It will be noted, however, that the four treatments fall into the same order for skin weight as for other tissues.

It is of interest to record that the experimental precision indicated from the foregoing analyses of variance is at an extremely satisfactory level, particularly in view of the small number of animals per treatment. The standard errors for bone, muscle, fat and skin of 3·9, 5·1, 8·9, and 6·1% respectively compare more than favourably with the usual figures for standard error per plot in the case of modern replicated experiments on agricultural crops (Wishart & Sanders, 1935), and with the type of figures obtained for carefully planned pig experiments using double the number of animals per treatment as has been the case here (Woodman et al. 1936).

The uniformity of the inbred animals used and the general design of the experiment have probably been the major contributing factors to the high standard of accuracy obtained.

No mention has been made of the relative effect as between the three major tissues; nor have we attempted to examine the many interesting implications of the relative treatment effects as a whole.

At the 16-week stage (Part II) we found that a low as compared with a high level of nutrition fell most severely upon fat and least upon bone. From Text-fig. 30 and from consideration of the foregoing data, it will be clear that at 200 lb. live weight, while fat remains the most restricted tissue by undernutrition (Low-Low) and the most favoured by good nutrition (High-High), the relative position of bone and muscle has been reversed.` Since bone and muscle for all treatments are "negative" relative to Low-Low, the tissue showing the greater negative difference has been affected relatively less than one showing a smaller difference. Thus as between these two extremes in treatment (Low-Low with High-High) we see that the Low-Low pigs have not only more than made up their 16-week deficiency in both bone and muscle, but that they have done so to a relatively greater extent in respect to muscle than bone. The latter has thus been penalized relatively more than muscle by long-continued under-nutrition. It might be argued that since the relative difference is small it may not be significant. It is of interest, however, that in the other two comparisons providing a direct measure of the effect of high and low nutrition from a common base line, Low-High with Low-Low and High-High with High-Low, a precisely similar

situation exists; in both cases the relative effect of the under-nutrition
has fallen more upon bone than upon muscle. It will later be shown that
a similar situation exists as between early- and late-developing parts of
the skeleton. The least that can be said, therefore, is that a long-continued
low level of nutrition, or its imposition after a period of adequate
nutrition, may lead to the elimination of the relative difference in effect
between bone and muscle apparent when the effects of under-nutrition
are examined at a younger stage of life. That this situation is perfectly
compatible with the theory that the differential effects of nutrition upon
composition are the result of the differential growth relationships existing
between the component tissues will be clear from the subsequent dis-
cussion.

At 16 weeks the effects produced by the different levels of nutrition
were capable of explanation on a basis of the prior claim to available
nutrients of those parts and tissues which from our age study we found
to be earlier developing. It is logical to assume that a similar explanation
should fit the facts in respect to the present series. With the late-
developing fat tissue and the earlier developing bone and muscle, this
is clearly the case. In the Low-Low pigs, under inadequate nutrition,
bone and muscle have continued to grow, and at the expense of fat. The
long duration of the process (327 days) has resulted in animals with
actually more bone and muscle and less fat than under any other treat-
ment. In the High-High treatment, ample nutritive supplies throughout
the growth period have encouraged the growth of all three tissues and
resulted in an animal with a well-balanced composition. Rapid growth
consequent on high nutrition has given full scope for the development
of bone and muscle, and the relatively short total period (165 days)
has not permitted an excessive growth of the later developing fat. The
change from a high to a lower level of nutrition in the High-Low treat-
ment (211 days) has allowed the continued growth of bone and muscle—
already well developed by the early good feeding and consequent rapid
growth—at the expense of fat and has resulted in pigs second only to
the Low-Low in bone and muscle with but little more fat. In the Low-
High treatment (211 days) we have the extremely interesting result that
not only has the change from inadequate nutrition to ample supplies
produced a marked recovery in the growth of all three tissues, but this
has been so great in respect of fat that the pigs of this treatment exceed
all others in their quantity of this tissue. This situation fits well our
general hypothesis and permits further elaboration. It would appear
that the stage of life over which the nutritional treatment is imposed
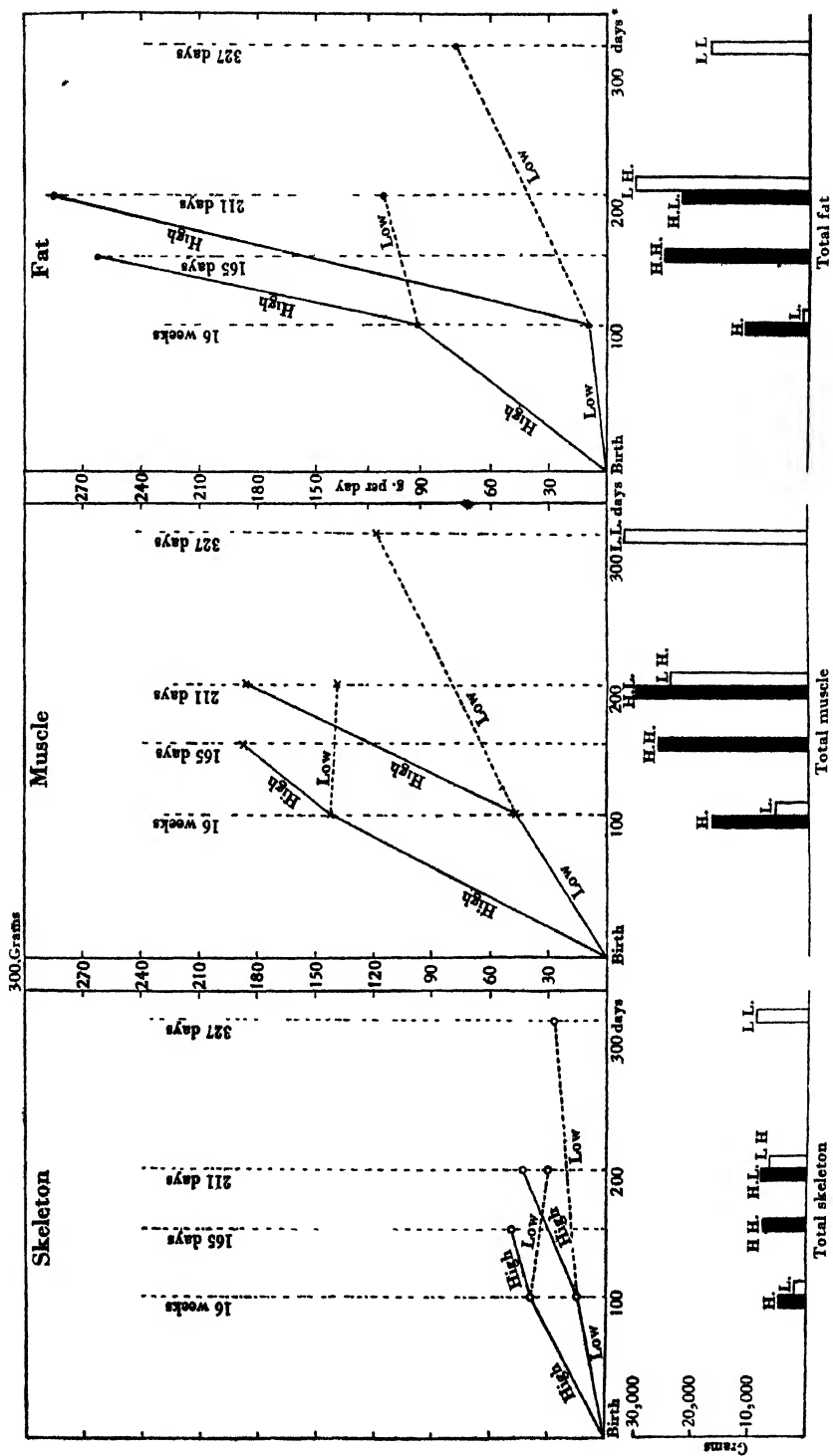
Text-fig. 31. Effect of plane of nutrition on rate of growth to 200 lb.

will affect the nature of the response. Thus in the Low-High treatment, the greater relative response of fat to the higher level of nutrition might be explained on the grounds that it occurred during a period when the growth intensity of bone and muscle is normally on the wane and that of fat on the increase. A similar explanation fits the facts noted above in the reversal of effect between bone and muscle. As growth proceeds it is possible to visualize a situation where, due to its natural decline in growth rate, the initially greater competitive efficiency of bone for limited nutritive supplies is transferred to the later developing muscle which thereafter gets a better chance to develop. This explanation receives support from a consideration of the rate of growth of the three tissues in grams per day (Table 44 and Text-fig. 31). The data represent mean rates for the periods covered and are based on the assumption that the pigs under consideration had the*same composition as those dissected at 16 weeks (Part II).

Table 44. *Rate of growth of skeleton, muscle and fat—g. per day*

Period ...	Birth—16 weeks		16 weeks—200 lb.			
Plane of nutrition ...	Low	High	High-High	High-Low	Low-High	Low-Low
Skeleton	15·98	38·45	49·28	30·0	44·1	27·82
Muscle	46·7	142·6	186·8	138·2	186·0	118·9
Fat	9·29	97·69	262·5	114·7	284·0	77·6
Age (days)	112	112	165·5	211	211	327
Period	112	112	53·5	99	99	215

In the Low-High treatment it will be observed that the recovery in the rate of growth of bone was insufficient to bring it to the level of the maximum rate attained by the treatment providing optimum conditions for its development (High-High). In muscle, however, recovery to the maximum rate was attained, while in fat the recovery rate exceeded the maximum shown by the High-High. Similarly, in the Low-Low treatment, continuation of the treatment beyond the 16-week stage produced a larger relative increase in the rate of muscle (from 46·7 to 118·9 g. per day) than in the rate of bone (from 15·98 to 27·82 g. per day). The relative increase in fat was even higher, indicating a still greater ability of this tissue to compete with age (from 9·29 to 77·6 g.). A similar position is shown by the other treatments (see above) showing a reversal in the relative effect of under-nutrition on bone and muscle.

At the same time, it is clear that associated with these differential responses, the time factor has exerted a big influence in determining the final composition of the pigs concerned. Even an extremely low rate of

growth continued long enough will permit an animal to attain good development of the tissue concerned. The Low-Low pigs illustrate this and the Low-High the reverse situation. In the latter, although the recovery in rate has been remarkable, the time interval has been insufficient for the pigs concerned completely to catch up in bone. Undernutrition has not inhibited the growth of any tissue—even fat—but has differentially slowed down the rate and altered thereby the differential relationships. All tissues are apparently capable of a considerable degree of recovery. In our animals the extent of this recovery in absolute terms has been dependent largely upon the time factor and the slaughter and comparison at an age when even the oldest is still relatively immature. This situation raises the question of the permanency of the effects produced, but this can be a matter only for speculation with our present data. They do provide, however, some evidence suggestive of a permanent effect in respect to bone.

(4) Effect upon organs

The mean weights and the relative effects on the body organs and offals are compared in Table 45 (main groups and total) and Table 46 (individual organs).

Table 45. *Plane of nutrition on development of organs* at 200 ℔*

Organs and offals	Mean weights (g.)				Proportion, Low-Low = 100			
	High-High	High-Low	Low-High	Low-Low	High-High	High-Low	Low-High	Low-Low
Skin, hair, hoofs	603	834	632	1257	48·0	66·3	50·3	100
Blood	4186	3930	3941	3813	109·7	103·0	103·3	100
Total glands	383	290	335	288	134·8	100·6	116·3	100
Thoracic organs	1585	1712	1641	1765	89·8	97·0	93·0	100
Abdominal organs:								
Alimentary tract	3365	3023	3047	3345	100·5	90·4	91 1	100
Remainder	5843	4868	6244	4705	124·2	103·5	132·7	100
Total	9208	7891	9291	8050	114·4	98 0	115·4	100
Total organs	16110	14767	15982	15252	105·6	96·8	104·8	100

* Including parts removed as offals.

In general, the effect has been such as might be expected from the behaviour of these·parts in the 16-week series. This is true of the individual components as well as of the total. High rates of growth in the pigs consequent on high nutrition have not produced any marked differential development in the total weight of organs which have attained almost the same proportions in the underfed animals. The relatively small differences apparent at 16 weeks have virtually dis-

appeared. The change to a high level of nutrition following early restriction has been accompanied by accelerated development of all organs and particularly those initially most retarded. Conversely, the change to a low level after early good feeding has produced little effect on organs with essential functions, though the growth of less essential parts has been penalized to a greater extent.

Table 46. *Plane of nutrition on development of individual organs* at 200 lb.*

Organs and offals	Mean weights (g.)				Proportion, Low-Low = 100			
	High-High	High-Low	Low-High	Low-Low	High-High	High-Low	Low-High	Low-Low
Hair and skin	528	758	564	1078	49·0	70·3	52·3	100
Hoofs: Fore	45	44	38	45	100·0	97·8	84·4	100
Hind	30	32	30	34	88·2	94·1	88·2	100
Blood	4186	3930	3941	3813	109·7	103·0	103·3	100
Neck thymus	132	92	128	77	171·4	119·4	166·2	100
Heart thymus	52	35	57	35	148·5	100·0	162·9	100
Lymphatic and salivary glands†	199	163	150	176	113·0	92·6	85·2	100
Diaphragm	409	455	406	480	85·2	94·8	84·5	100
Heart	286	272	270	297	96·3	91·6	90·9	100
Pericardium and blood vessels	221	262	322	324	68·2	80·8	99·4	100
Lungs and trachea	669	720	648	664	100·8	108·4	97·6	100
Oesophagus	53	65	55	89	59·6	73·0	61·8	100
Stomach	569	595	540	728	78·2	81·7	74·2	100
Small intestine	1603	1235	1413	1377	116·2	89·7	102·6	100
Caecum	141	144	135	135	97·2	105·9	100·0	100
Large intestine and rectum	1001	986	905	1016	99·5	97·4	89·1	100
Caul	135	131	180	128	107·8	102·3	140·1	100
Mesentery	1129	1035	1200	1003	112·5	103·3	119·6	100
Liver	2438	1763	2253	1842	132·4	95·7	122·3	100
Gall bladder	46	26	39	37	124·0	70·3	105·4	100
Spleen	88	81	81	84	104·8	96·4	96·4	100
Pancreas	114	97	122	105	108·6	92·4	115·2	100
Kidneys	401	282	378	294	146·4	103·0	137·9	100
Kidney and leaf-fat	1444	1400	1933	1179	122·5	118·7	164·0	100
Bladder	52	53	51	54	96·3	98·1	115·4	100
Uterus and vagina	203	236	198	288	70·5	81·9	68·8	100
Penis and vesiculae seminalis	86	93	109	70	122·8	132·8	155·7	100

* Including parts removed as offals.
† Including lymphatics of body, but excluding those of alimentary canal.

In the abdominal group, differences in the alimentary tract are small, but in the "remainder" are larger and all treatments exceed the Low-Low. This is due to the relatively greater effect of nutrition upon the late-developing fat-containing parts and to specialized effects upon livers and kidneys. Differences in the thoracic group are small and in a negative direction relative to Low-Low; here also the position is affected by the

differential response of individual components. Blood shows but small differences and those that exist are in line with our previous explanation; the quantity is slightly 'greater in' animals on a higher metabolic level (Part II). Large differences are apparent in respect to total glands— due to the precocious behaviour of the thymus—and in skin, hair and hoofs. In the latter, the difference is due mostly to epidermis and hair, and the effects were also clearly visible in the live animals. The poorly fed pigs had long coarse hair and a relatively harsh and scaly skin. The well-fed pigs had soft, pliable skins and fine silky hair. Change from good to poorer nutrition in the High-Low treatment was accompanied by a change in the character of the skin and hair toward that of the Low-Low pigs. This can also be detected in the relative weights. The result is in line with the function of these parts.

Of the individual organs of the thoracic group, the heart and lungs have proved relatively resistant. The diaphragm has even attained absolutely greater proportions in the Low-Low pigs than in the remainder. This may have been due in part to the extremely active life of these pigs relative to the placid existence of the well fed. The former were continually on the move, though confined, in their vociferous demands for food. It was noted also that whereas the diaphragm of the well-fed pigs contained a high proportion of fat, those of the Low-Low and to a lesser degree the High-Low, were predominantly muscle. The oesophagus – another muscular organ—was relatively best developed in the Low-Low pigs. Both the latter points are in line with the relative increase with age in the competitive capacity of muscle for an inadequate nutritive supply.

Table 47. *Effect of plane of nutrition on length of alimentary tract at 200 lb.*

	Mean length (cm.)				Proportion, Low-Low = 100			
Part	High-High	High-Low	Low-High	Low-Low	High-High	High-Low	Low-High	Low-Low
Small intestine	2186	2087	2143	2015	108·5	103·5	106·4	100
Caecum	23	25	22	22	104·5	113·6	100	100
Large intestine and rectum	482	479	490	520	92·7	92·1	94·2	100
Total length	2691	2591	2655	2557	105·2	101·3	103·8	100
Total weight (g.)	2743	2364	2452	2528	108·5	93·5	97·0	100

Of the individual abdominal organs, the units of the alimentary tract show relatively small differences in the direction expected in both weight and lengths (Table 47). The pigs finishing on a High Plane have slightly heavier and longer tracts. Parts showing large differences are the caul,

mesentery, and kidney and leaf-fat, where the order Low-High, High-High, High-Low, and Low-Low is the same as for total carcass fat and in line with the relationship between nutrition and fat of which these parts mostly consist. Note that as with internal fats at 16 weeks, the relative effect is less than upon carcass fats.

The pancreas similarly has been influenced in a manner compatible with its metabolic function and its behaviour at 16 weeks.

The female genital organs are relatively heavier in the Low-Low and High-Low—the older pigs. Remembering that at 16 weeks low nutrition had considerably penalized these organs, it would appear that age has had an influence here. The Low-Low animals at 327 days are past the normal age of puberty which usually occurs at from 180 to 250 days, so that this result is in line with the functional relation of nutrition effects. It might be noted that though ovulation had not occurred in any animal of the series, the ovaries of all contained large and numerous follicles. Though delaying, under-nutrition has not inhibited sexual development. High nutrition does not appear to have advanced it. Accelerated development occurred in the pigs changed to a High Plane after 16 weeks, though the time interval before slaughter has evidently been insufficient to permit the organs of these pigs to attain the proportions of the chronologically and physiologically older animals. Relative differences in the urogenital organs of the castrates are in line with their loss of sex function and the larger amounts of unremoved fat on the parts concerned in the well-fed pigs.

Table 48

A. *Analysis of variance of liver (g.)*

Variation	Degrees of freedom	Sum of squares	Mean square	
Between treatments	3	1,530,528	510,176·0	$Z = 1·3058$ S.S.
Between sets	4	381,479	95,369·8	
Error	12	449,354	37,446·2	
Total	19	2,361,361	—	

B. *Analysis of variance of kidneys (g.)*

Variance	Degrees of freedom	Sum of squares	Mean square	
Between treatments	3	66,867·8	2,2289·3	$Z = 1·1490$ S.S.
Between sets	4	38,939·0	9,744·75	
Error	12	26,878·2	2,239·85	
Total	19	132,685·0	—	

S.S. = significant at 1 % point.

Owing to the special interest attaching to the behaviour of the liver and kidneys at 16 weeks, their differential response to the varying treatments has been analysed in greater detail and the significance of the differences tested by analysis of variance (Tables 48 A, B). The resulting interrelationships of the treatments are shown in Table 49.

Table 49. *Table of significance—kidneys, liver and thymus*

	High-High	High-Low	Low-High	Low-Low
		Kidneys		
High-High	**405·4**	S.S.	N.S.	S.S.
High-Low	S.S.	**288·6**	S.	N.S.
Low-High	N.S.	S.	**374·4**	S.S.
Low-Low	S.S.	N.S.	S.S.	**267·8**
		Liver		
High-High	**2454·2**	S.S.	N.S.	S.S.
High-Low	S.S.	**1786·0**	S.S.	N.S.
Low-High	N.S.	S.S.	**2205·2**	S.S.
Low-Low	S.S.	N.S.	S.S.	**1825·0**
		Thymus		
High-High	**184·6**	S.S.	N.S.	S.S.
High-Low	S.S.	**119·0**	S.S.	N.S.
Low-High	N.S.	S.S.	**185·2**	S.S.
Low-Low	S.S.	N.S.	S.S.	**111·6**

S.S. = significant at $P < 0.01$.   S. = significant at $P < 0.05$.   N.S. = not significant.
The mean is shown in heavy type.

Treatment effect upon the liver has been strongly significant at the 1% level. The standard error per pig is 193·4 g. or 9·35% of the mean. The standard error of the treatment means is 86·5 g. Treatment differences are similarly highly significant in respect to kidneys. The standard error per pig is somewhat higher at 47·3 g. or 14·1% of the mean. Standard error of the treatment means is 21·16 g.

In both livers and kidneys, the High-High and Low-High treatments have produced heavier organs than either Low-Low or High-Low. The differences are all strongly significant at the 1% point except as between the kidneys of the Low-High and High-Low pigs, where the former are significantly heavier at the 5% level. Neither of the two treatments producing the heavier livers and kidneys, nor the two producing the lighter, differ significantly.

The differences are extremely large. Thus the heaviest kidneys, produced by the High-High treatment, have a mean weight of 405·4 g. For pigs of the same body weight reared on normal rations, Woodman *et al.* (1936) give 250 g. as the mean kidney weight. This is comparable with the average of 267·8 g. of our Low-Low treatment which yielded the lightest kidneys.

It will be evident from the treatment relationships that we can extend somewhat the hypothesis advanced in respect to the effect of the treatment upon these organs up to the 16-week stage. At this age the High-Plane pigs produced kidneys with a mean weight of 283 g.—heavier than normally fed pigs of twice the body weight and 310% heavier than the 16-week Low-Plane pigs. This difference was attributed to the high protein content of the rations used. This high kidney growth has continued in the High-High pigs; reduction of the amount of feed in the High-Low animals over a 100-day period has resulted in no significant increase in kidney weight over their size at 16 weeks, though body weight has doubled in the interval; the change to a High Plane of feeding over the same period in the Low-High pigs has resulted in a tremendous relative increase in the weight of the kidneys to a level little below that of the High-High pigs; continuation of a Low Plane of feeding in the Low-Low has produced kidneys within the range of weight of those of normally fed animals. The situation is comparable in liver weights. For all these, the rations have been qualitatively the same and exceptionally rich in protein. It seems, therefore, a reasonable conclusion that the functional adaptation of the kidneys and livers of pigs to high protein rations is correlated closely with the gross protein intake and not necessarily with the percentage of protein in the ration. It is possible to feed a highly rich protein diet without kidney hypertrophy providing the quantitative plane of nutrition is on a low level, nor will initial hypertrophy continue on the same ration if its quantity is reduced. The plane of nutrition, the protein content of the ration and the rate of growth of the pig would all appear to affect the situation by their part in determining the amount of excess protein to be deaminated. In respect to the liver its glycogenic function, probably more than its part in deamination, will likely have been involved in determining its weight response. Larger amounts of glycogen will have been stored by the livers of pigs on a High Plane of nutrition. Photographs of the kidneys concerned are shown in Pl. 20, where the relative differences in size are clearly apparent. All are to the same scale. Note the parallelism between the variation within treatments and the individual live-weight growth curve. One abnormal pair occurred in pig 93. This is a condition similar to that recorded in one case in the 16-week series except that, in addition to a developmental difference common to both, a tumour was also present. The writer is indebted to Dr J. R. M. Innes of the Institute of Animal Pathology, Cambridge, for the following report:

"*Kidney Pig No. 93—Embryonal Carcinoma.* This organ showed

a moderate degree of retention of the foetal lobulation. In addition at one pole there was a large white opaque mass of tissue projecting well above the normal margins; on section it was found to be deeply embedded in the kidney tissue though sharply demarcated from it. There were also a few small retention cysts. Histological examination showed this tissue to be a tumour of the type recognized as an 'embryonal carcinoma' and thus not unlike the Wilm's tumour of children. According to American authors this is an apparent frequent type of tumour in pig's kidneys. The condition is a purely coincidental autopsy finding which has with certainty no relation to the high plane of protein nutrition. The organ has functioned efficiently."

The pig concerned showed good growth on change to a high level of nutrition, and it is of interest to note that the weight of the kidney responded similarly to those of other pigs on the same treatment.

The data provide further interesting evidence of the relation between the thymus gland and the nutrition of the animal. This organ exhibits the same direct correlation with the plane of nutrition as do the kidneys and livers; its weight is increased by a High Plane and decreased by a Low. The thymus of both the High-High and the Low-High pigs exceeds that of the Low-Low and High-Low by more than 50%. That the situation is not due to the age differences, and that the weight of the thymus is not a direct function of age, is clearly apparent from its behaviour under the High-Low and Low-High treatments. At 16 weeks its mean weight in the former pigs was over 500% greater than in the latter. Now, at the same age and weight, its weight in the latter exceeds that in the former by 50%. The statistical relationships have been worked out for this organ also and are shown in Table 50 (analysis of variance) and Table 49 (table of significance). The standard error of the treatment means is 8·9 g. All the differences referred to are significant at the 1% level, while those between the two treatments yielding the heavier, and the two yielding the lighter, are not significant. The position supports our previous suggestion that any relation between the thymus and growth is indirect rather than direct.

Table 50. *Analysis of variance of thymus (g.)*

Variation	Degrees of freedom	Sum of squares	Mean square	
Between treatments	3	24,736	6,189·0	$Z = 1·3650$ S.S.
Between sets	4	7,151·5	2,383·8	
Error	12	4,844·5	403·7	
Total	19	36,732·0		

S.S. = significant at 1% point.

The relative effects upon the early-developing organs of the head, the eyeballs and brain, are in line with their relative high insensitivity to the influence of nutrition (Table 51). The eyeballs of the oldest pigs (Low-Low) are significantly heavier than those of all other treatments. Those of the youngest pigs (High-High) are the lightest. There is some slight evidence of a nutritional effect as between High-Low and Low-High where the weight difference is just significant at the 5% point at 2·14 times its standard error. Our previous conclusion, however, that age is the dominant factor in respect to the development of the eyes is fully borne out by the data. Similarly, the brain has continued to show marked resistance, though to a lesser degree, to nutrition, but the influence of age is definitely apparent. The weight difference between the High-Low and Low-High treatment, in favour of the pigs well fed in early life, is significant at the 1% level and would indicate that nutrition can exert some influence on brain growth.

Table 51. *Effect of weight of eyeballs and brain at 200 lb.*
(*Treatment means*)

	High-High	High-Low	Low-High	Low-Low	Mean	Standard error
Eyeballs	11·2	12·2	11·4	13·8	12·15	0·264
Brain	98·0	115·6	98·6	113·8	106·5	2·416

Summing up the position, the picture here presented provides further substantial evidence of the relative resistance of the vital organs to varying quantitative nutritive planes. As parts essentially concerned with the maintenance of life, they are capable of claiming a proportionately large share of, an inadequate food supply than are later developing and less essential body tissues. What differential response to nutrition is noticeable is similarly capable of explanation on a functional basis. Under a limited nutritive supply, growth gives way to function, and under an ample supply those organs, whose functions are more directly associated with growth, are benefited relatively more. The special sensitivity of certain organs to qualitative differences in nutrition provides a further example of the functional basis of organ response. ·

(5) Effect upon skeleton

Mean weights of the major skeletal groups and the proportional effects of the treatments relative to Low-Low are compared in Table 52.

In total skeleton, the four treatments showed increasing weight of tissue in the order, Low-High, High-High, High-Low, and Low-Low.

This order holds with marked regularity for the individual bone groups. There is only one obvious exception—the thoracic vertebrae of the High-High and High-Low, where the order is reversed and the weight is a few grams in favour of the former. These are the two treatments, the difference between which in total skeleton is not statistically significant though the trend is in line with our general hypothesis.

Table 52. *Plane of nutrition on development of skeleton at 200 lb.*

Part of body	Mean weights (g.)				Proportion, Low Plane = 100			
	High-High	High-Low	Low-High	Low-Low	High-High	High-Low	Low-High	Low-Low
Head:								
Tongue bones	9.7	9.4	8.3	11.4	85.1	82.5	72.8	100
Lower jaw	361	391	363	481	75.0	81.3	75.5	100
Skull	1036	1069	1001	1259	82.3	84.9	79.5	100
Atlas	62	67	60	77	80.5	87.0	70.2	100
Axis	52	54	48	61	85.2	89.0	73.8	100
Vertebral column:								
Cervical	213	225	185	237	89.9	94.9	78.0	100
Thoracic	703	697	582	737	95.4	94.6	79.0	100
Lumbar*	358	426	345	421	85.0	101.2	86.8	100
Sacral*	133	139	108	155	85.8	89.6	78.6	100
Ribs and sternum	965	994	851	993	97.2	100	85.7	100
Pelvis	422	441	362	467	90.4	94.4	77.3	100
Forelimbs (2)	1446	1544	1286	1585	91.2	97.4	81.1	100
Hindlimbs (2)	1375	1445	1183	1506	91.3	95.9	78.6	100

* Variable number of vertebrae. See Appendix IV.

In respect to the relative effects *within* treatments, our explanation of the reversal in the order of effect as between total bone and muscle would imply either a reduction or even an elimination of the differences which we would otherwise expect to find between early- and late-developing skeletal units. We have postulated that due to the normal decline with age, in the growth intensity of the earlier developing tissue (bone), the competitive capacity for a continued inadequate nutritive supply of the later developing tissue (muscle), is relatively increased. If this be sound it is logical to expect a comparable situation to exist between early- and late-developing bones. The decline with age in the intensity of growth of the earlier developing bones will be relatively greater than in the later, which under both a continuation of the same nutritive conditions and a change to a higher level will be able to secure a greater proportion of the supply and be afforded a chance to recoup their initially greater weight deficiency. The extent to which they will succeed will depend upon the time interval involved and the extent of the initial repression.

Consideration of the interrelationships available in Table 52 shows

that this is the case. In general we find that, relative to a High Plane of nutrition, there has been either no greater or even less retardation of the late-developing parts of the Low-Plane skeletons. This is the case in each of the three such comparisons available. (Note that though absolute weights are higher in the Low-Low, the greater the deficiency of the others relative to Low-Low, the less the proportionate "retardation". effect in the latter.)

At first sight the pelvis appears to provide an exception to this situation. Between the extreme treatments, High-High and Low-Low, pelvis weights are nearer each other than are the earlier developing head bones and have thus been restricted by the low level of feeding relatively more than the latter. The pelvis is one of the latest developing bones and in consequence was stimulated most by high nutrition at 16 weeks—a relative effect likely to be still more pronounced in the High-High at 200 lb. The position is thus quite compatible with the above if we postulate, in addition, that in the Low-Low pigs even the long time interval available has been insufficient for a very late-developing bone to make up its deficiency to the same degree. That is, the increasing share of available nutrients to late-developing units, while encouraging their growth relatively more during later ages, may be insufficient for the *latest* developing to alter the relative order of effect apparent at younger stages of growth. Note that as between Low-High and Low-Low, elimination of the difference in effect upon skull and pelvis has occurred. Here, with no initial leeway between pelvis weights to make up, since they started from a common base-line at 16 weeks, both treatments have encouraged pelvis growth relatively more than skull growth. This has allowed equalization in effect, the time interval in this case being too short for the pigs changed to a higher level of feeding to attain pelvis weights which would place them in the same relative position as the High-High, Low-Low comparison.

That after 16 weeks—an arbitrary age fixed only by the limits of our data—late-developing parts *do* make greater proportional growth on both High and Low Planes of nutrition is clearly illustrated by the data of Table 53. These incidentally provide confirmatory evidence of the existence of growth gradients up the limbs as discussed in Parts I and II.

Detailed data for the limb bones are given in Table 54. These are in agreement with the position discussed above; the four treatments fall in the same order for individual bone weights, and the alteration in the order of effect as between late- and early-developing units is apparent. With respect to the latter the agreement between the two limbs

Table 53. *Relative growth of early- and late-developing skeletal units under varying planes of nutrition*

	Relative effect of nutrition at 16 weeks		Relative increase over respective weights at 16 weeks			
	Low Plane	High Plane	High-High	High-Low	Low-High	Low-Low
Hindlimb:						
Cannons	100	224	137	148	264	320
Femur	100	221	151	160	285	377
Pelvis	100	245	170	177	354	458
Forelimb:						
Cannons	100	210	144	158	264	320
Humerus	100	223	153	168	306	400
Scapula	100	283	163	165	406	464
Skull	100	209	158	163	326	402

Table 54. *Plane of nutrition and development of skeleton at 200 lb.*
(Bones of limbs)

	Mean weights (g.)				Proportion, Low-Low = 100			
	High-High	High-Low	Low-High	Low-Low	High-High	High-Low	Low-High	Low-Low
Forelimbs (2):								
Cannons	94	103	82	99	94·9	104	82·9	100
Splints	27	28	22	28	96·4	100	78·6	100
Carpals	77	85	72	83	92·8	102	86·7	100
Radius-ulna	327	347	294	355	92·1	97·7	82·8	100
Humerus	485	537	435	568	85·4	94·5	76·6	100
Scapula	322	326	284	325	99·1	100	87·4	100
Total leg	1332	1426	1189	1458	91·2	97·5	81·3	100
Pedals	15·0	15·7	12·5	17·4	86·2	90·2	71·8	100
Naviculars and sesamoids	9·8	10·9	8·8	11·3	86·7	96·5	77·9	100
Coronets	24·8	26·0	21·2	27·0	91·9	96·3	78·5	100
Pasterns	41·1	44·9	36·3	44·7	91·9	100·4	81·2	100
Dew claws	23·8	23·7	19·2	25·4	93·7	93·3	75·6	100
Total foot	114·5	121·2	98·0	125·8	91·0	96·2	78·3	100
Hindlimbs (2):								
Cannons	104	113	90	109	95·4	103·0	82·6	100
Splints	25	27	22	26	96·2	103·8	84·6	100
Tarsals	56	60	49	58	96·6	104·0	84·5	100
Calcaneum	77	80	67	79	97·5	101·0	84·8	100
Astragalus	67	70	57	66	101·5	106·0	86·4	100
Tibia-fibula	386	408	332	427	90·4	95·6	77·8	100
Patella	31	33	27	32	96·8	103	84·4	100
Femur	522	553	445	589	88·6	93·9	75·6	100
Total leg	1268	1344	1089	1386	91·3	96·9	78·5	100
Pedals	12·9	14·1	11·6	15·2	84·8	92·7	76·3	100
Naviculars and sesamoids	8·6	9·9	7·4	10·0	86·0	99·0	74·0	100
Coronets	25·1	26·7	21·8	27·1	92·6	98·5	80·7	100
Pasterns	42·5	46·8	38·2	46·1	92·2	101·5	82·9	100
Dew claws	20·1	19·3	15·7	21·4	95·2	90·2	73·4	100
Total foot	109·2	116·8	94·7	119·8	91·2	97·8	79·0	100

is striking. The nutritional effect decreases in the order, cannons, radius-ulna and humerus in the forelimb, and cannons, tibia-fibula and femur in the hind, with an increase between these bones and the scapula and pelvis respectively.

Treatment effects upon bone form and size are illustrated in Pls. 21–26, which compare to the same scale (4 cm. square background) some of the more important and typical skeletal units of every pig in the experiment.

In Pl. 21 the capacity of the plane of nutrition to influence the form of the skull is clearly evident. In respect to size, the treatments producing the heaviest skulls, Low-Low and High-Low in that order, also give the largest. Differences in form consist mostly in the degree of development of the nasal bones which contribute largely to the extra length of the pigs finishing on a lower plane of nutrition. This is specially the case in the Low-Low where the skulls are absolutely longer and relatively narrower than on any other treatment. A High Plane of nutrition has produced short, broad skulls even when the animals were subjected to a low level of nutrition in early life (Low-High) and which during that period developed relatively most in linear proportions (Pl. 10).

Differences in the size and form of the ribs (Pl. 22) are similarly very marked, though weight differences between the treatments were not great (Table 52). This is due to the differential treatment effect upon length and thickness growth. Pigs on a Low Plane throughout show extremely long and thin ribs. Approaching these are the High-Low, where reduction in nutrition during the later stages of growth has allowed length growth to continue relatively more than thickness. A High Plane throughout, on the other hand, has resulted in short, thick ribs, while the change from a Low Plane to a High has not been accompanied by as great a response in length growth as in thickness. Note the difference in the "spring" of rib consequent on these influences. In this connexion pig 93, which shows the latter to an exaggerated degree, is not quite comparable with the remainder as the animal had a marked curvature of the spine (see Pl. 17) which probably influenced the rib spring. From a practical point of view these rib differences are important in evaluating the "depth of chest" measure of carcass quality (see § 8, and Part IV, § 3).

The lumbar vertebrae (Pl. 23) show the same type and order of treatment effect; the Low-Low and High-Low having the longest and largest lumbar columns. It will be noted that some variation exists in the form of the first and last lumbar. Thus in pigs 106 and 82, the first lumbar has some of the characteristics of a thoracic vertebrae in that it provided posterior attachment for the last rib, of which these two animals had

an unusually high number (17 and 16 pairs respectively). It retains in both cases the transverse processes and the typical spinous process of a lumbar however. In pig 74, which also has an extra pair of ribs, we find the opposite situation in that the last lumbar has some of the characteristics of a sacral vertebrae. Situate partly in the lumbar and partly in the sacral region it was attached to the pelvis and yet showed large transverse processes, positionally malformed. The condition is comparable to the lumbarization of the first sacral vertebrae found in humans (Harris, 1937). These are the three pigs which, following our jointing practice (see Dissection technique), gave loins with only five lumbar. Examination of the other cases showing the higher number of ribs (16 + pair) indicates that in every case some tendency toward modification of either the first or last lumbar has occurred (pigs 84, 107, 72 and 73). Shaw (1929), from X-ray examination, records a variation of from five to seven in the number of lumbar vertebrae.

These observations raise questions of the relationships between rib number and length of loin of pigs. Breeders have long been interested in increasing the length of pigs by increasing the rib number (Shaw, 1930), and have achieved considerable success. If the addition of ribs—which may vary from thirteen to seventeen pairs—leads to a reduction in the vertebral number and length of the most valuable part of the animal— the loin—breeding on a basis of rib number will not be advantageous from the carcass-quality angle. Extra length is not required in the thoracic region. It is obviously desirable to obtain more precise information as to the anatomical implications of increasing rib number. Working in this laboratory, Palsson (1939) has found similar variations in the lumbar vertebral number in sheep (five to seven) with comparable modifications of the first or last associated with a variable rib number. He has also found one case with a reduction to six in the normal number of cervical in consequence of the attachment of the first rib to the last cervical. From the genetic point of view, it is of interest to note that recent dissection of the foundation boar of the strain (no. 338, Appendix 1), and the sire by whom most of the pigs in this experiment were bred, showed fifteen pairs of ribs and the sixth lumbar with some of the characteristics of a sacral.

Pl. 24 shows the effect upon the pelvis. The differences are large and clear-cut between treatments and show excellent uniformity within treatments. The Low-Low and High-Low have produced the largest, and the High-High and Low-High the smallest, the order being the same as that in weight. So far as we have been able to assess without precise

measurement, no abnormalities in shape exist between the different treatments. The differences lie in relative size. The writer is indebted to Prof. H. R. Harris of the Anatomy School, Cambridge, for confirmation in this opinion. The small pelvis of the Low-High pigs is fairly typical of that of the immature animal, while that of the Low-Low approaches the form of the mature pig. At the same time similar differences to those already mentioned in respect to length and thickness of bones under the four treatments will be observed, i.e. in the High-Low and Low-Low the bones are relatively longer and more slender than in the High-High and Low-High where, in that order, they are relatively short and broad. The latter, of course, are the most slender in absolute terms.

The femurs are shown in Pl. 25. Note the correlation between these and relative leg lengths of Pls. 17–19. Note also that the epiphyses are much the same size in each treatment, though they also show the same treatment effect, and that the difference lies mainly in length and width of the shaft. To illustrate that the individual bone units have been influenced in the same manner as the skeleton as a whole, the statistical relationships of the treatment effects upon the weight of the femur have been compared by analysis of variance (Table 55), and to state in more precise terms the effects upon bone form, the length of the femurs has been measured. These also are compared statistically (Table 56).

Table 55. *Analysis of variance of femurs (weight, g.)*

Variation	Degrees of freedom	Sum of squares	Mean square	
Between treatments	3	13,505·75	4,501·92	$Z = 1·8262$ S.S.
Between sets	4	552·30	138·10	
Error	12,	1,400·50	116·7	
Total	19	15,458·55	—	

S.S. = significant at 1 % point.

Table 56. *Analysis of variance of femurs (length, mm.)*

Variation	Degrees of freedom	Sum of squares	Mean square	
Between treatments	3	3,130·4	1,043·467	$Z = 1·8222$ S.S.
Between sets	4	222·5	55·625	
Error	12	327·1	27·258	
Total	19	3,680·0	—	

S.S. = significant at 1 % point.

In both weight and length, treatment effects are highly significant at the 1 % level. The standard errors per pig are 10·8 g. or 4·09 % of the mean, and 5·21 mm. or 2·6 % of the mean respectively. Standard errors for the treatment means are 4·83 g. and 2·33 mm.

The significance of the treatment differences are shown in Table 57. In weight, all six comparisons show the same relationships as provided by total skeletons; five differ significantly and one is not significant. In length, also, five comparisons differ significantly at the 1 % level while one is not significant. It will be observed, however, that a change has occurred. Whereas the High-Low femur, like the High-Low skeleton, is heavier but not significantly heavier than the High-High femur, the length differences between these two treatments are strongly significant at 5·1 times their standard error. On the other hand, the High-High femur, like the High-High skeleton, though significantly heavier than the Low-High, is not significantly longer.

Table 57. *Table of significance—weight and length of femur*

	High-High	High-Low	Low-High	Low-Low
Weight of femur (g.)				
High-High	**260·6**	N.S.	S.S.	S.S.
High-Low	N.S.	**274·8**	S.S.	S.
Low-High	S.S.	S.S.	**222·4**	S.S.
Low-Low	S.S.	S.	S.S.	**295·2**
Length of femur (mm.)				
High-High	**177·4**	S.S.	N.S.	S.S.
High-Low	S.S.	**194·2**	S.S.	S.S.
Low-High	N.S.	S.S.	**182·2**	S.S.
Low-Low	S.S.	S.S.	S.S.	**209·8**

S.S. = significant at $P < 0.01$. S. = significant at $P < 0.05$. N.S. = not significant.
The mean is shown in heavy type.

This situation provides further useful evidence in respect to the relative effect of nutrition upon length and thickness growth of bone. As between the High-High and High-Low, continued high nutrition has encouraged thickness growth rather than length (the late- rather than the early-developing character), while in the High-Low the change to a lower nutritive level has allowed length growth to continue but penalized thickness growth to some extent. The bones in consequence differ more in length than in weight. Similarly, as between High-High and Low-High, the change to a higher level of feeding has enabled the latter to regain their initial length disadvantage, but though thickness growth, which was penalized relatively severely at 16 weeks, has recovered considerably, the time has been insufficient for it completely to eliminate the difference, and the resulting bones are lighter and more slender than the pigs on a High Plane throughout the period.

The weight, length and thickness (weight/length) relationships between the treatments are summarized in Table 58. Note that the High-High pigs show the highest thickness index, and the Low-High the

lowest. Low-Low and High-Low fall into intermediate positions in that order. The agreement between these effects and those of Chirvinsky (1909) as to the slendering influence of low nutrition upon bone growth may be noted. The thickness index has also increased considerably with increased weight, that of the High Plane pigs at 16 weeks being 110.

Table 58. *Effect of plane of nutrition on weight
and form of the femur. Summary*

	High-High	High-Low	Low-High	Low-Low	Standard error*
Weight (g.)	260·6	274·8	224·0	295·2	4·83
Length (mm.)	177·4	194·2	182·2	209·8	2·33
Weight/length	146·9	141·5	122·9	140·7	—

* Standard error of treatment mean.

Pl. 26 illustrates the effects upon the hind cannons. Similar differences to those already noted are apparent here.

Summarizing the position, it is clear that the plane of nutrition is capable of exerting considerable differential effects even upon the relatively early-developing and "resistant" skeleton; these effects are apparent in both weight and form, and are capable of explanation on a basis of the differential growth relationships existing between the skeleton and other tissues on the one hand, and between the various skeletal units on the other.

(6) Effect upon muscle in different parts of the body

The mean weights, and the proportional effects, of the four treatments upon the musculature of the different anatomical regions of the body are set out in Table 59.

The treatments have affected the muscle weights of the different parts in the same manner as the total weight of this tissue, the absolute weights increasing in the order, Low-High, High-High, High-Low, and Low-Low. This order holds for practically every joint. The only exceptions are the loin muscles, which are lower in the High-High than the Low-High pigs by a few grams, and the muscle round the cannon bones in respect to which slight variations are apparent. The former case is due to the presence in the High-High treatment of two pigs (106 and 74) with only five lumbar vertebrae which reduced the weight of muscle in their respective loin joints by approximately one-sixth as compared with the normal. Correcting for this, the mean loin muscle weight for the High-High treatment becomes 2310 g., and the normal order of treatment effect holds. Note that the psoas muscle of the loin region, which is

unaffected by lumbar variation, exhibits the normal order. The variations in the cannon muscle are likely due to the relatively high dissection error associated with this muscle which is not only small in size, but which is difficult to separate satisfactorily from its attachments.

Table 59. *Effect of plane of nutrition on development of muscle in different parts of body*

Part of body	Mean weights (g.)				Proportion, Low-Low = 100			
	High-High	High-Low	Low-High	Low-Low	High-High	High-Low	Low-High	Low-Low
Head	996	1080	986	1353	73·6	79·8	72·9	100
Neck	2486	2846	2078	2940	84·6	96·8	70·7	100
Shoulders (2):								
Shoulder	4817	5331	4311	5592	86·1	95·3	77·1	100
Arm	506	606	459	619	81·7	97·9	74·1	100
Cannon	26	36	26	37	70·3	96·2	70·5	100
Total	5349	5973	4796	6248	85·6	95·6	76·3	100
Thorax	6401	7066	5698	7608	84·1	92·9	74·9	100
Loin:								
Psoas	665	758	626	753	88·3	100·7	83·1	100
Loin	2136	2546	2178	2550	83·8	99·8	85·4	100
Total	2801	3304	2804	3303	84·8	100	84·9	100
Legs (2):								
Thigh	5499	6433	4987	6681	82·3	96·3	74·6	100
Leg	1006	1177	911	1180	85·3	99·7	77·2	100
Cannon	35	48	36	53	66·0	90·4	67·0	100
Total	6540	7658	5934	7914	82·6	96·8	75·0	100
Pelvis	2041	2130	1732	2406	84·8	88·5	72·0	100

In respect to the relative effect within treatments, it is of interest to observe that unlike the skeletal units the different units have been influenced in the same way as at 16 weeks. Those parts which at this age were penalized most by inadequate nutrition, or stimulated most by rapid live-weight growth consequent on good feeding have been similarly influenced to a larger extent by the varying planes of nutrition. Note that, as with bone, since all muscle units relative to Low-Low are negative, the larger the deficiency of other treatments from the latter the smaller the retardation effect of under-nutrition upon the Low-Low part.

Thus maximum effect has fallen upon the muscles of the loin region and minimum upon those of the head. Between High-High and Low-Low, for example, we can account for the difference in relative effect on the grounds that under the limited nutritive supply of the latter, head muscles have continued to grow proportionately more than the later developing loin while, in the High-High, the latter muscles have been

stimulated to a greater extent. The same situation exists as between early- and late-developing units of the forelimbs where the gradient in effect from the cannon muscles (least affected) to the shoulder muscles (most affected) is well defined in each treatment. This gradient is not so well marked in the muscles of the hindlimb where the thigh units show a smaller influence than expected.

The comparison afforded by the High-Low and Low-High are of special interest from the carcass-quality angle. In all parts of the body, weight of muscle is greater in the High-Low, while the relative differences are greater in respect to the later developing and more valuable parts of the animal. Good nutrition in early life has encouraged muscle development as a whole and in the more valuable parts, and a change to a lower level of feeding in the later stages of growth has still permitted considerable muscular development. In the Low-High, however, poor feeding in early life has penalized muscle to a large extent, but while the change to better nutritive conditions has produced considerable recovery, this has been insufficient to allow the pigs to make up their initial deficiency compared with the former treatment by the time they reached bacon weight.

It will be recognized that the order of nutritional effects apparent at lighter weights (16 weeks) as between early- and late-developing parts has been retained in these heavier and older pigs. This result is in line with the maintenance of a higher rate of growth in muscle tissue for a longer period than is the case with bone (see Part I). Even the earliest developing units will still be capable of extensive growth at the older ages, and the decline in the relative intensity of growth between these and later developing units, postulated in the case of bone, will not be likely to have occurred to the same extent. The analogy between this situation and the "latest" developing bone units (pelvis and scapula), which also retained the expected order of effect, might be noted.

(7) Effect upon fat in different parts of the body

Treatment effects upon subcutaneous fat, intermuscular fat and total fat for the individual joints are shown in Table 60. Note that the quantities for the head and neck joints have been pooled in each case. This is in consequence of jointing errors which tended to be reflected in the distribution of fat between these two parts.

In both tissues, the effect between the four treatments is the same for the individual joints as for total carcass fat. The quantity increases

in the order, Low-Low, High-Low, High-High and Low-High. As might be expected from its behaviour at the 16-weeks stage, these effects are much greater than on either bone or muscle of the same regions. In all cases, too, subcutaneous fat has been influenced to a greater degree than intermuscular, a result supporting our previous conclusions respecting their relative order of development (Parts I and II).

Table 60. *Effect of plane of nutrition on development of fat in different parts of body*

Part of body	Mean weights (g.)				Proportion, Low-Low = 100			
	High-High	High-Low	Low-High	Low-Low	High-High	High-Low	Low-High	Low-Low
Head and neck:								
Subcutaneous	2440	2211	2932	1665	147	132·7	170·3	100
Intermuscular	1370	1622	1887	1370	100	118·3	134·8	100
Total	3810	3833	4819	3035	126	126·2	154·6	100
Shoulders (2):								
Subcutaneous	2228	2023	2637	1553	143·5	130·3	169·8	100
Intermuscular	929	764	888	799	116·3	95·6	111·0	100
Total	3157	2787	3525	2352	134·0	118·5	149·9	100
Thorax:								
Subcutaneous	5870	4728	6614	3537	166·0	133·6	187·1	100
Intermuscular	3009	2551	3445	2185	137·7	116·8	157·7	100
Total	8879	7279	10059	5722	155·1	127·2	175·8	100
Loin:								
Subcutaneous	2580	2194	3348	1537	167·9	142·7	218	100
Intermuscular	468	567	598	422	110·9	134·4	141·7	100
Total	3048	2761	3946	1959	156·0	140·9	201·4	100
Legs (2):								
Subcutaneous	2756	2806	3189	2134	129·1	131·5	149·4	100
Intermuscular	506	493	565	507	100	97·2	111·4	100
Total	3262	3299	3754	2641	127·3	125·0	142·2	100
Pelvis:								
Subcutaneous	2569	2062	2703	1746	147·1	118·0	154·8	100
Intermuscular	353	337	400	331	106·6	101·8	120·8	100
Total	2922	2399	3103	2077	140·6	115·4	149·3	100

If our hypothesis in respect to the behaviour of the early- and late-developing muscle units is sound, we would expect, in respect to the still later developing fat, that even more markedly the order of effect of high and low nutrition on the fat in different parts will be the same as that exhibited at 16 weeks, i.e. late-developing areas will show greater retardation under low nutrition and greater stimulation under high.

Since all treatments show *more* fat than the Low-Low, the greater the difference of other treatments from the latter the greater the treatment effect upon the part concerned. It will be observed that in all treatments relative to Low-Low, larger differences exist between the

amount of fat in the later developing loin region than between the earlier head and neck joints. Thorax falls into an intermediate position, with the effect on the pelvis less than upon the loin. For the trunk joints this is identical with the order of development apparent from the age series (Part I) and the order of effect of the plane of nutrition at 16 weeks (Part II). In all cases, too, the fore- and hindlimbs exhibit their relatively early-developing character.

As between the three treatments providing a comparison of high and low nutrition from a common base-line, good feeding has produced marked acceleration in the development of the fat in the later developing parts, while on inadequate or lower levels, fat deposition in these has been relatively retarded (High-High and High-Low, High-High and Low-Low, and Low-High and Low-Low). When a high level of nutrition has followed an initial inadequate level as in the case of the Low-High, the growth of fat in the late-developing regions, as also with total fat, has been tremendously accelerated. We see in this evidence of the tendency exhibited by bone and muscle in respect to the increased competitive capacity of late-developing parts with age. It will be remembered that this tendency was also exhibited by the fat as a whole in the Low-Low treatment (see Text-fig. 31). In the latter treatment, too, this effect is apparent in respect to the joints, the relative increase in the subcutaneous fat of head and neck as compared with the loin being 9 times and 22·3 times their respective 16-week weights. Comparable figures for the Low-High pigs are 15·8 times and 48·5 times. Even the High-Low treatment shows a slightly greater relative growth of the loin fat as compared with the head and neck from 16 weeks.

Although this tendency even on inadequate rations exists, it will be recognized that so great is the fat response to high nutrition, it is the latter rather than the former which controls the relative effects at 200 lb. Fat deposition, as previously emphasized, is not subject to the same growth limitations as bone and muscle, and the extent of its development depends largely upon the surplus nutrition available after the prior claims of these tissues have been satisfied. From this point of view it might be considered that fat should not be regarded as true growth. It is abundantly clear, however, that even under inadequate nutrition supplies, fat deposition occurs; moreover, it is an inseparable accompaniment of live-weight growth in the animal body. In part, at least, therefore, fat formation must be considered as true growth.

(8) Effect upon carcass measurements

Treatment effects upon carcass measurements are compared on the same basis as employed for other characters in Tables 61 (external measures and streak), 62 (fat measures) and 63 (muscle and fat measures on loin cut) (see Text-fig. 2).

Table 61. *Plane of nutrition on body and carcass measurements at 200 lb.*

	Mean measurements (mm.)				Proportion, Low-Low = 100			
	High-High	High-Low	Low-High	Low-Low	High-High	High-Low	Low-High	Low-Low
Body length	1067	1098	1052	1100	97·0	99·8	95·6	100
Carcass length	762	790	748	767	99·3	102·9	97·5	100
Length of leg	567	606	565	626	90·5	96·8	90·3	100
Depth of chest	349	350	351	352	99·0	99·3	99·7	100
Forearm length	217	228	207	232	93·5	98·3	89·2	100
Forearm circumference	233	232	226	232	100	100	97·4	100
Length of trotter	95	106	90	97	94·1	105	88·6	100
Streak:								
Chest	30	32	28	28	107	114·2	100·0	100
Middle	27	33	29	28	96·4	118·9	104·6	100
Inguinal	27	31	32	28	96·4	110·7	112·9	100

An examination of the precise relationship of these measures to carcass quality is presented in Part IV; at this stage it is sufficient to emphasize that, as indicated by their relative behaviour under varying nutritive planes, they bear to a greater or lesser degree definite relationships to carcass composition.

Thus, in respect to the major external linear measurements which are indicative probably more of the degree of skeletal development of the animal than anything else, the differences due to treatment are relatively small as compared with fat measures, and are comparable with treatment effects upon bone growth. They are comparable with the latter, too, in respect to the order of effect between treatments. Thus the heaviest boned treatments (Low-Low and High-Low) have yielded the longest pigs—as measured by both body length and carcass length, with also the longest legs as measured by leg length, foretrotter length, and forearm length. These results support the picture of conformation differences obtained from the photographic comparisons of the animals (Pls. 17–19) and the differences in length of the bones of trunk and limbs (Pl. 23–26).

Since the treatment effects follow the same trend as related effects on composition already dealt with, the statistical significance of the differences noted have not been tested except in the case of carcass

length. The latter is of special importance as a qualitative measure in both pork and bacon pigs, while it is also one of the few measures recorded by workers who have considered the quality aspects of nutritional effects. Treatment effects are significant at the 1 % level. The standard error per pig is 17·64 mm. or 2·3 % of the mean. The standard error of the treatment means is 7·89 mm. The High-Low pigs are significantly longer than both High-High and Low-High animals at the 1 % point, but are not significantly longer than the Low-Low. Other differences are not significant.

Several workers claim an association between growth rate and length of carcass. Hansson (1927) found that the longer type of pig had the faster growth rate. Scott (1930), working with large numbers and several breeds of widely different type, also obtained longer carcasses from pigs making the highest daily gains. The latter were, however, also the heavier pigs, and for this reason would tend to be longer (Hammond & Murray, 1937). Callow & Davidson (1933), with more homogeneous material, report that pigs of the long type had a faster growth rate. The short-type animals were also overfat at bacon weight (Callow, 1935 b). Other workers have not found any association between growth rate and length. Hogan *et al.* (1925) obtained no significant differences between the growth rates of long and short pigs using breeds of different types (Large White and Poland China). Carroll (1929), also with different breeds, found that while extremely short types had a slower growth rate than the longer intermediate type, the longest type of all had a still slower rate. Evvard (1929), under self-feeding conditions, obtained larger daily gains from the small type pigs than the large. Lush (1936a), with Danish Testing Station data, obtained a negative correlation between growth rate and length, while Rijssenbeek (1936), with similar material from Netherland stations, records greater length where the rate of live-weight growth was slower during the later stages of fattening.

In none of the above cases has there been any critical experimentation on the point, which has been incidental to other and major issues. The comparisons made, too, have been between different types of pig rather than between different growth rates and the conflict of opinion is explainable on these grounds. The small type of pig (pork breed) is a shorter animal at the same weight than the large type (bacon breed) (Hammond & Murray, 1937), and the greater rate of growth in absolute terms (lb. per day) of the latter (Whetham, 1934) will necessarily give, but not necessarily be responsible for, the association claimed between high rate and high length when different type animals are compared.

In the homogeneous sample of this experiment both a high rate of growth and a very slow rate has resulted in relatively short carcasses. A high rate following an initial "stunting" period has produced an even shorter animal. Only an initially high rate followed by a slow has had any marked effect in increasing length. Since the length measure involved is one of length of the spinal column, the reason is apparent. The differentially lower response of bone to good nutrition has meant that the extremely rapid growth to bacon weight of the High-High, though encouraging, has given insufficient time for any extensive length development. The effect is exaggerated in the Low-High, for bone growth was somewhat retarded by under-nutrition during the period when it normally grows most rapidly (g. per day), and subsequent rapid increase in live weight occurred when the rate of bone is normally falling. In the High-Low, on the other hand, advantage was taken of the early rapid phase in bone growth by providing good nutrition, and the extra time provided by the slowing down of the growth in live weight allowed length growth to continue. We have in effect advanced development in the two former treatments and obtained animals comparable to the small pork type. In the latter, development has been retarded and resulted in the production of the extreme bacon type animal. This situation, and indeed the results of this experiment as a whole, provides strong experimental support for Hammond's (1935) picture of the fundamental differences between the pork (early-developing) and bacon (late-developing) breeds and types, and for his analogy between the manner of growth of each and the differential effects upon growth of a high and low level of nutrition respectively.

Streak measurements show no significant treatment differences and no definite trend in their behaviour. This is not unexpected for several reasons; the small number of pigs per treatment and the relatively high margin of error associated with this measure would necessitate large differences for any effect to show up; further, and more important, the effect of "fasting" in increasing the thickness of the streak (Callow, 1935b) would tend to reduce the difference otherwise likely—on account of the fat content of the belly—between the treatments finishing on a Low Plane and those finishing on a High Plane. Though no differences are thus apparent in thickness of the streak, the composition of the area differs markedly, the Low-Low and High-Low pigs having a much greater proportion of muscle to fat (Pl. 27).

The treatment effects upon the thickness of back fat (Table 62) are extremely large and in line with the effect upon weight of fat as a whole

Table 62. *Plane of nutrition on subcutaneous back fat
measurements at* 200 *lb.*

	Mean measurements (mm.)				Proportion, Low-Low = 100			
	High-High	High-Low	Low-High	Low-Low	High-High	High-Low	Low-High	Low-Low
Shoulder fat:								
Outer	8·4	8·9	10·6	9·0	93·3	98·9	117·7	100
Inner	32·7	29·6	40·2	27·0	121·1	109·6	148·9	100
Total	41·1	38·5	50·8	36·0	113·8	107·2	141·1	100
Loin fat:								
Outer	8·4	6·6	11·0	5·7	147·3	115·8	193·0	100
Inner	15·4	10·5	20·1	8·0	192·5	131·2	251·3	100
Total	23·8	17·1	31·1	13·7	173·0	124·8	227·0	100
Rump fat:								
(1) Anterior	37·3	27·6	38·5	21·0	177·6	131·4	183·3	100
(2) Median	28·2	20·1	33·3	12·5	225·6	160·8	266·4	100
(3) Posterior	35·5	28·5	41·3	18·8	188·8	151·5	219·6	100
Mean	33·7	25·4	37·7	17·4	192·1	145·1	215·4	100
Mean back fat	32·9	27·0	39·9	22·4	147·0	121·0	178·9	100

and in the different parts of the body. The influence upon the earlier
developing shoulder fat is less than on measures toward the hind-end
of the body. In all cases, too, the effect upon the outer layer of fat is
less than upon the inner layer and the gradient in effect upon each, in
an anterior-posterior direction, is well defined. These results are in agree-
ment with the order of development of the parts concerned and their
relative behaviour under high and low nutrition at 16 weeks.

Table 63. *Plane of nutrition on measurements
on loin cut at* 200 *lb.*

	Mean measurements (mm.)				Proportion, Low-Low = 100			
	High-High	High-Low	Low-High	Low-Low	High-High	High-Low	Low-High	Low-Low
Muscle:								
Length of eye *A*	78·1	86·0	73·5	89·9	86·9	95·7	81·8	100
Depth of eye *B*	37·1	40·4	36·8	39·5	93·9	102·3	93·2	100
Shape index— *B/A* × 100	476	470	500	442	107·6	106·3	113·1	100
Fat:								
At *C*	24·1	18·2	30·4	11·2	215·0	162·6	271·4	100
At *H*	36·1	24·9	42·2	18·8	192·0	128·0	224·4	100
Skin thickness	3	3	3	3	100·0	100·0	100·0	100

Effects upon the muscle measures on the loin cut (Table 63) are
likewise large and consistent with the relative degrees of muscular
development of the pigs concerned. Low-Low and High-Low treatments
show the larger eye muscles. As with total muscle, all treatments show

lower measures than the Low-Low. The one exception—the B measure of the High-Low—illustrates the relatively greater stimulation of this measure compared with A by high nutrition. All other treatments show the same effect, the A measure being relatively less retarded in the Low-Low pigs than B. This situation is reflected in the "shape index" under each treatment which is higher—indicating a relatively deeper eye muscle—in all three treatments compared with the Low-Low.

The highest shape index is shown by the Low-High pigs despite absolutely smaller measurements for both A and B. This is due to the relative greater increase after 16 weeks in the depth measure, under the stimulus of high nutrition; an interesting confirmation of the observations already made that a change from a low to a higher level accelerates most the growth of late-developing parts.

These results provide strong support for the hypothesis (Hammond, 1933, 1936b) that the development of a large depth of eye measure is closely dependent upon a high level of nutrition. They are not, however, entirely consistent with the argument arising from this situation (Hammond, 1934) that the "defective" development of the eye muscle so frequently met with in pigs (see also Callow, 1935a) possibly results from inadequate nutrition during the early stages of life when muscle is normally developing rapidly. That there is some such connexion is clear from the nature of all our results, but in the Low-High pigs, though the eye depth is least in absolute terms, its recovery from what has probably been a greater degree of stunted development than normal even under bad husbandry has been remarkable. It is possible of course that we are working with animals with high genetic capacity for muscle growth, and that the combination of the type of treatment to which the Low-High pigs have been subjected with poor hereditary capabilities in this connexion might have produced the defect referred to. A further possibility is that the high level of protein nutrition employed in this experiment might have exerted some correcting influence, and permitted a degree of muscle recovery not possible under the lower levels of protein feeding normally employed in practice. The very great practical importance of the problem, together with the desirability of investigating the nature of the response of the body to qualitative as well as quantitative nutritional differences, has prompted us to test the latter hypothesis in a subsequent experiment (see Addendum to Part III). Though the results of this await detailed analysis, there appears little grounds to believe, however, that the plane of protein nutrition of itself exerts any marked influence upon the development of the eye muscle.

Influence on the fat measures on the loin cut (Table 63) are even higher than on back-fat thickness (Table 62), the treatments falling in the same order as for the latter and as for weight of fat. The results would support the contention of Hammond & Murray (1937) that because of the late-developing character of the region, pigs should be examined at the loin if maximum differences in composition are to be detected. It will be observed that relative to Low-Low, fat at H has been affected less than fat at C. This result is somewhat at variance with the order of development of these two measures and their relative response at 16 weeks. It is due probably to the fact that in the Low-Low pigs the eye muscle was very much tapered at its lower point (Pl. 27), and this tended to exaggerate the length of the H measure in these pigs. In support of this it will be noted that as between the High-High and High-Low providing a similar nutritive comparison, H has been retarded relatively more than C by the lower plane of nutrition. Skin thickness provides no measurable treatment differences.

Photographs of the loin cut section are shown in Pl. 27 (A, males; B, females). These are all to the same scale—same eye-muscle length (measure A)—and in consequence provide a comparison of the relative proportions of fat to muscle under the four treatments as well as of the relative differences in eye-muscle shape.

As already discussed, the Low-Low pigs have long shallow eye muscles, comparable to the Low Plane at 16 weeks and the shape in very young animals. In other treatments depth of eye is better developed. In fat, the relative treatment effects are well defined and follow the order of effect upon weight of fat. Note that what variability exists follows the differences in the shape of the individual growth curves and sex. Thus the fastest growing Low-High male (pig 89) has the most fat, while its High-Low counterpart (pig 85), which had to be grown more rapidly after 16 weeks to keep pace, has also more fat than the other High-Lows. The only marked lack of uniformity in effect in Pl. 27 A occurs in respect to pig 93 which is a female; note, however, that even with sex against the comparison it has a higher proportion of fat than its High-Low counterpart (pig 98), and that it presents a very uniform picture with the other females on the same treatment. Even the Low-Low pig making the most rapid rate of growth (pig 71) shows this in its slightly high proportion of fat.

(9) Effect on histology and colour of muscle

As at 16 weeks and for the same reasons (Part II, § 9) histological examination of the treatment effect upon muscles has been confined to the measurement of fibre diameter size in the longissimus dorsi, and to the examination of the development of marbling, or intramuscular fat, in the same muscle.

Technique has been as given in Part I, § 9. The mean fibre diameter size of each pig together with the standard error of the fifty fibres measured in each case is given in Table 64. The treatment mean together with its standard error has been calculated in each case from the mean measurements for each pig.

Table 64. *Effect of plane of nutrition on size of muscle fibre (longissimus dorsi) at 200 lb.*

(Mean diameters of 50 fibres per pig—1/6 and 4 eyepiece)

High-High		High-Low		Low-High		Low-Low	
Pig no.	μ	Pig no.	μ	Pig no.	μ	Pig no.	μ
70	16·64 ±0·42	72	16·72 ±0·53	73	14·88 ±0·45	71	18·36 ±0·61
83	15·78 ±0·49	85	17·80 ±0·52	89	14·46 ±0·55	99	17·60 ±0·59
106	15·04 ±0·51	99	16·80 ±0·55	93	14·60 ±0·52	107	17·44 ±0·64
74	16·74 ±0·56	103	19·44 ±0·77	79	14·20 ±0·50	82	16·72 ±0·47
84	15·92 ±0·48	67	17·44 ±0·69	66	16·66 ±0·59	80	17·70 ±0·72
Mean	16·02 ±0·34	Mean	17·64 ±0·49	Mean	14·96 ±0·44	Mean	17·56 ±0·26

Differences noted in weight of muscle are clearly evident also in the size of the fibres, the Low-Low and High-Low treatments having larger fibres than the other two treatments which yielded the smaller amount of muscle. Note that the Low-High shows the smallest fibres and the smallest weight of this tissue. Statistical relationships have been calculated and the analysis of variance (Table 65 A) shows treatment effects to be strongly significant at the 1 % level. The standard error per pig is 0·9104 or 5·5 % of the mean, and the standard error of the treatment means 0·407.

The treatment interrelationships are similar to those for muscle weight (Table 65 B). Both High-Low and Low-Low have significantly larger fibres than either of the other treatments, but do not themselves differ significantly. Nor do the High-High and Low-High differ significantly. In the two latter comparisons, differences in weight were significant only at the 5 % point. Though providing a similar picture, fibre size has thus not been as sensitive as weight differences in detecting differences in muscle development. This is understandable in view of the relatively

high variability in fibre diameter within any one muscle and the practical difficulties of measuring more than a limited number. Differences in fibre size are illustrated in Pl. 28 together with those of the comparable 16-week High and Low Plane pigs from which they have been "derived". The comparisons afforded provide a good illustration of the capacity for recovery in muscle growth under the stimulus of high nutrition after initial retardation, and of the capacity of this tissue for long-continued growth under conditions of an inadequate nutritive supply.

Table 65 A. *Analyses of variance of muscle fibre size* (μ)

Variation	Degrees of freedom	Sum of squares	Mean square	
Between treatments	3	25·2153	8·4051	$Z = 1·5543$ S.S.
Within treatments	16	13·2604	0·8288	
Total	19	38·4757		

S.S. = significant at 1% point.

Table 65 B. *Table of significances —muscle fibre size*

Mean (μ)	High-High	High-Low	Low-High	Low-Low
High-High	16·02	S.	N.S.	S.
High-Low	S.	17·64	S.S.	N.S.
Low-High	N.S.	S.S.	14·96	S.S.
Low-Low	S.	N.S.	S.S.	17·56

S.E. = 0·407 μ.

S.S. = significant at 1% point.   S. = significant at 5% point.   N.S. = not significant.

In respect to marbling fat (Pl. 29) all pigs of the two treatments producing the larger amounts of carcass and internal fats (Low-High and High-High) showed more intramuscular fat on histological examination than the leaner pigs of the Low-Low and High-Low. Some individuals of the latter have fairly large quantities, though it was impossible to differentiate between these two classes. No satisfactory measure of the differences has been found except that of grading the individual sections by eye when they fell into the above two broad groups. The photographs of Pl. 29, which are negative prints with the fat in consequence showing white, illustrate the general picture presented. It will be noted that these results are supported by the chemically extracted fat from the thorax muscle of the four treatments, though in the latter case differentiation between the two fats and the two lean treatments is well defined and follows their general order of fatness (see § 10). Note that the Low-Plane 16-week pig shows a negligible amount of marbling fat, and the High-Plane a relatively large amount.

In respect to colour of muscle (Table 66), the results presented are in

line with our previous discussions of this character. The more active muscle (diaphragm) is darker in colour than the less active (longissimus dorsi) illustrating the effect of exercise, while rapid growth (High-High) has produced a lighter coloured muscle, even in the diaphragm, than slow growth (Low-Low) illustrating the effect of age. In the latter the muscles were so like beef muscles in colour that they were hardly recognizable as pork.

Table 66. *Effect of plane of nutrition on colour of muscle at 200 lb.*

	High-High					High-Low				
Pig no. ...	70	106	83	84	74	85	72	98	67	103
Diaphragm	6 P	5 P	10 B	10 B	11 B	10 B	11 B	11 B	11 B	10 B
Longissimus dorsi	3 P	2 P	2 P	3 P	4 P	2 P	5 P	4 P	3 P	5 P

	Low-High					Low-Low				
Pig no. ...	89	73	93	66	78	71	107	99	80	82
Diaphragm	11 B	10 B	11 B	11 B	10 B	11 B	12 B	11 B	11 B	11 B
Longissimus dorsi	2 P	3 P	4 P	4 P	4 P	10 B	10 B	10 B	10 B	10 B

P = pork scale (pale).   B = beef scale (dark).   1 = pale.   12 = dark.

Note that between pigs of the same age there are no significant differences in colour of either muscle, though the longissimus dorsi tends to be slightly darker in the High-Low, probably due to the more active life of the hungry animal. The change to a high level of nutrition has completely changed the muscle colour of the pigs concerned (Low-High) which at 16 weeks was relatively dark. This result may be interpreted as a consequence of the reduction in exercise following the elimination of hunger, the well-fed animal leading a much less active existence than the hungry.

(10) Effect upon chemical composition of muscle and fat

For the reasons already given (see Part II, § 10) the chemical data available are confined to representative samples from one set of hogs and one of gilts, i.e. two pigs on each of the four treatments.

The mean results on a percentage basis are set out in Table 67. The muscle data cover the psoas muscle and a sample from the longissimus dorsi at the junction of the thorax and loin. The fat data is in respect to subcutaneous only, and in each case covers the inner and outer layer from the same region as the thorax muscle sample. As mentioned previously, these samples provide a reasonable picture of the chemical composition of the total muscle and fat tissues.

The percentage of intramuscular fat is highest in the Low-High, and lowest in the Low-Low pigs, with the High-High and High-Low occupying intermediate positions in that order. This is the same order as for total amount of fat tissue. There are two exceptions to this position; both the Low-Low hog and gilt have a higher percentage fat than the corresponding High-High animals in the psoas muscle. There is no apparent reason for this, since the opposite situation is the more reasonable expectation in view of the relative rates (absolute) of fat deposition. In the thorax muscle, the treatment differences are better defined. Note also the differences in fat content of hogs and gilts are in favour of the former and consistent with the higher rate of fat growth in the hog than in the gilt pig (see Sex differences).

Table 67. *Effect of plane of nutrition on chemical composition of muscle and subcutaneous fat at 200 lb.*

| | | | Muscle | | | | | | | |
| | | | Psoas | | | | Thorax (longissimus dorsi) | | | |
	Pig no.	Plane of nutrition	Fat %	Tissue %	Water %	Iodine no.	Fat %	Tissue %	Water %	Iodine no.
Hogs	70	High-High	2·63	20·53	76·84	63·5	4·87	24·09	71·04	57·7
	72	High-Low	3·40	21·52	75·08	65·3	3·58	23·68	72·74	60·5
	73	Low-High	5·50	20·72	73·78	57·2	9·15	21·68	69·17	54·5
	71	Low-Low	4·26	20·24	75·50	71·0	2·04	24·31	73·65	68·0
Gilts	84	High-High	2·24	20·54	77·22	70·3	4·15	23·32	72·53	60·7
	67	High-Low	2·72	21·74	75·54	68·3	3·66	23·84	72·50	60·9
	66	Low-High	3·40	21·41	75·19	·63·8	4·67	23·57	71·76	57·4
	80	Low-Low	2·61	21·02	76·37	70·1	2·01	24·16	73·83	65·6

| | | | Subcutaneous fat | | | | | | | |
			Outer layer				Inner layer			
Hogs	70	High-High	88·98	2·19	8·83	63·9	88·93	2·90	8·17	58·1
	72	High-Low	91·44	2·35	6·21	64·4	93·56	1·60	4·84	56·9
	73	Low-High	87·15	2·74	10·11	59·4	92·42	1·35	6·23	54·6
	71	Low-Low	88·32	2·90	8·78	71·4	89·78	2·36	7·86	66·1
Gilts	84	High-High	87·69	3·27	9·04	65·0	90·36	2·46	7·18	57·3
	67	High-Low	88·22	3·25	8·53	'68·2	87·88	3·03	9·09	61·3
	66	Low-High	89·63	2·59	7·78	60·9	92·65	1·79	5·56	54·4
	80	Low-Low	82·50	4·36	13·14	69·5	86·98	3·58	9·44	60·8

Differences in water content and in tissue percentage are in line with the differences in fat content. The figures for iodine value are of considerable interest in relation to the soft fat problem, while the design of the experiment affords an excellent opportunity for testing the theory of Callow (1935*a*, *b*) that the degree of saturation of the fat is intimately dependent upon the rate (in absolute terms) of fat deposition. On this basis it would be expected that the iodine values would fall into the

treatment order, Low-Low, High-Low, High-High and Low-High. The observed values agree quite well with this position, though there are two modifications in the gilt series.

In the subcutaneous fat, differences in the percentage fat are not so well defined between treatments, though the pigs finishing on a lower plane tend to have a lower fat content in both inner and outer layers. As in our age series and at 16 weeks, the inner layer has the higher fat content. As with muscle, the water content follows an opposite treatment trend, being higher in those with a lower fat content. Moulton (1920) and Hoagland & Powick (1925) with steers, Mitchell & Hamilton (1929) and Ellis & Zeller (1934) with pigs, have shown comparable effects to these in the effect of food restriction on the chemical composition of lean and fat tissues.

Table 68. *Chemical composition of foodstuffs used*

	% fat*	Iodine no.	% dry matter	% crude protein
Barley meal	3·14	117·2	90·6	9·26
Flaked maize	1·26	114·6	90·35	8·86
Middlings	4·12	116·0	91·25	13·95
Milk powder	0·04	42·5	93·83	37·44
Fish meal	1·62	169·5	92·65	67·25

* Solvent petrol ether A.R. 40–60° B.P.

The iodine values of the back fat exhibit the same general tendency as those of the intramuscular fat. The Low-Low treatment in all cases, and in both inner and outer layers, has yielded pigs with more unsaturated fat than those from other treatments. Conversely, the Low-High treatment has produced the most saturated fat in all cases. The treatments expected to yield intermediate results do so though they vary somewhat in their relative order. Whether this situation involves the operation of additional factors to those implied by the "growth theory" must remain for further data to elucidate. One or two points may be noted, however. The difference between the fat metabolism of hogs and gilts may in part be responsible; the latter have a much slower rate of fat deposition (in absolute terms), and since this is apparently related to sex functions (Hammond, 1932a and § 2) it is conceivable that the nature as well as the quantity of the fat between the sexes may vary so far as their specific response to nutrition is concerned. The type of food, as implied by the theory, is a dominant factor and in this experiment (Table 68) the ration has been such as to reduce the effect of fast and slow growth respectively upon the degree of saturation of the fat deposited. The oil content of the

ration has been low and its quality high from the soft fat point of view. Further, the fat intake of the individual animals, by virtue of the design of the experiment, has not been controlled. These factors, together with the individuality of the animal—and genetic factors have been postulated by Lush (1936 b) as possibly operative in fat quality in the pig—together with the sampling errors associated with the few individuals so far chemically examined might easily account for the variations from the expected order of treatment effect referred to above. In any case the differences could not be expected to be large owing to the rations used.

It must be emphasized that the foregoing represents but a preliminary and tentative statement of the effects upon chemical compositions and may be subject to modification when complete data are available. Hilditch *et al.* (1939) have recently published an account of the chemical composition of the fats of the pigs in this series; they find that in the Low-Plane pigs the fat is softer due to an increase in the proportion of linoleic acid present, together with some increase in the proportions of oleic acid.

(11) Sex differences in composition

Reference has been made at several points to the fact of sex differences in carcass composition. It is not our intention to describe in detail the many differences in anatomical characters which exist between hogs and gilts, but a brief discussion of the major variations in composition is relevant to our general thesis.

The absolute and relative amounts of bone, muscle, and fat (mean values) in the carcasses of the hogs and gilts in each treatment are shown in Table 69 A.

From these data it is clear that gilts are characterized by less fat, more bone, and more muscle than are hogs. The differences are shown in each treatment, are of considerable magnitude, and are influenced by the plane of nutrition. Examination of the data for the individual pigs (Appendix IV) shows that in general these differences in weight are uniformly apparent in the separate anatomical units of the three tissues concerned as well as in the total quantity.

The fact of sex differences in the amount of fat in the body of pigs of the same weight has been recognized by several workers. Thus, using carcass measurements as indices of the general state of fatness, Hansson & Bengtsson (1926) with Swedish pigs, Lacy (1932) with American breeds, Murray (1934) with English breeds in South Africa, and Berge (1936) with the Large White and Landrace, consider the hog pig to carry more

fat than the gilt. Similarly, Woodman *et al.* (1936) with the Large White and Hammond & Murray (1937) with the major English breeds record the same result. The former workers also obtained larger muscle measurements from the carcasses of gilts than that from hogs, and considered this to indicate a higher degree of muscle development in the female. They obtained confirmation of this result by balance experiments (Woodman *et al.* 1937) which showed the gilt to have a greater nitrogen retention than the hog. On the other hand, Mitchell & Hamilton (1929) report no difference in the chemically estimated fat content of the two sexes, while Olson & Bull (1931) on a basis of cutting yields claim the slight tendency toward greater fatness of the hog to have been insignificant. Whether these contrary opinions are due to differences in carcass weight and/or to technique is not clear, but there can be no doubt that the gilt pig at the same carcass weight may be markedly different in carcass composition from the castrate male. Providing the animals are comparable in other respects—breed, nutrition, etc.—this is such that the gilt has less fat and more bone and muscle. That environmental conditions (nutrition) to which the animals have been subjected are capable of considerably modifying this situation, even to the extent of reversing it, is clear from Table 69 A. On the other hand, the sex differences are consistently less in the two extreme treatments—High-High and Low-Low—than in the other two treatments, and on the other, the hogs of the Low-Low treatment have considerably more bone, more muscle. and less fat than the gilts of the Low-High treatment. Other similar comparisons can be made. This provides a possible reason for the differences of opinion noted above; in both studies, differences in the shape of the growth curves of the individual pigs concerned appear to have existed.

Table 69 A. *Effect of sex on composition of carcass at 200 lb.*

Treatment		High-High		High-Low		Low-High		Low-Low	
		Weight g.	Proportion	Weight g.	Proportion	Weight g.	Proportion	Weight g.	Proportion
Total skeleton	♂	6930	100	7159	100	5978	100	7888	100
	♀	7186	103·7	7890	110 2	6819	114·1	8141	103·2
Total muscle	♂	25059	100	27434	100	22669	100	31782	100
	♀	27664	110·4	32676	119·1	25407	112 1	31761	99·9
Total fat	♂	25590	100	25242	100	32177	100	18476	100
	♀	24502	95·7	19469	77·1	26231	81·5	17095	92 5

While little definite evidence is available, it is a matter of common observation that the entire male pig has heavier bones and less fat than

entire females. Hammond & Murray (1937) present a limited amount of data on this point in a comparison of the four sexes in the Large White breed. Castrated males and females had thicker back-fat measurements than the corresponding entire animals, while the entire female had more fat than the entire male. In other species also the normal female appears to have more fat than the normal male. This has been demonstrated in poultry by Mitchell *et al.* (1926), in rats by Morris *et al.* (1933), in rabbits by Wilson & Morris (1932), and in sheep by Hammond (1932a) and Palsson (1939). Hammond (1932a) reviews the literature in respect to sex differences in bone in different species. The male has longer, thicker and heavier bones than the female, and castration of the former postpones ossification, prevents thickening growth and causes a slightly increased length growth. It is somewhat surprising, therefore, to find in our data that the castrate males have lighter and smaller bones than comparable gilt pigs. Gramlich & Thalman (1930) have obtained apparently contradictory results to ours in respect to fat. Working with cattle, they report that while spayed heifers had more fat than normal heifers, the latter were fatter than steers. It is possible that there is a species difference, not necessarily in the nature of the response to castration but in the degree of the response. It is clear, for example, that castration in either sex will increase the amount of fat in the body; whether the increase will be sufficient to alter the order of the difference between the sexes may depend upon the difference in endocrine balance produced by removal of the sex organs which may vary with species. A complete understanding of the results of castration must await solution of the many fundamental problems concerning the function, behaviour, and interrelation of the glands of internal secretion.

From our data it will be observed that the differences in the amount of muscle and fat indicate that the hogs have stored a considerably greater amount of energy than the gilts in carcasses of the same weight. This raises the rather interesting point that the differences between the two sexes may be regarded as being due to a difference in the "physiological" level of nutrition, so far as the major body tissues are concerned. It is generally accepted that the use to which nutrients are put by the animal body is largely under hormonic control; in the sexually active female as compared with the sexually inactive castrate, a smaller total proportion of the nutrients absorbed are directed toward bone, muscle, and fat formation. In consequence the female is on a relatively lower level of nutrition in respect to these tissues. This is not incompatible with a higher rate of general metabolism in the gilt. It is significant that

the relative behaviour of the tissues concerned in the two sexes supports this hypothesis; as with a low "external level of nutrition", a greater proportion of the available nutrients goes in the female to the earlier developing bone and muscle than to the later developing fat. The relative differences between the sexes on the two extreme treatments would lend additional support to this in that both a very high and a very low external level of nutrition has tended to reduce the sex difference.

Whatever may be the physiological mechanism responsible for the differences, it is clear that these exist to an extent sufficient to warrant attention from the carcass-quality angle. In competitions and litter testing of bacon pigs for breed improvement these facts should be taken into account. It is also important to emphasize that in experimental treatments involving consideration of the effects upon the body, attention must be directed to sex in planning and interpretation.

(12) Discussion

The continuation of variations in the level of nutrition (shape of the growth curve) to a more advanced stage of development, so that differences in body weight and in some cases in age have been eliminated, provides evidence no less striking than at 16 weeks of the power of the nutritional environment as a controlling force in respect to the form and composition of the animal body. This is seen not only in the marked differences between animals on extremely high and low levels, between these and animals changed from a high to a low level during the later stages of growth, but also in the marked recuperative capacity shown by all tissues in their response to high nutrition following initial retardation.

Different tissues are at different relative stages of development at any moment in time, and common slowing down or speeding up in the rate of growth of the whole affects them differentially. Growth is not arrested by under-nutrition; its rate is altered and the period of growth prolonged. The stage of development determines the effect of the alteration. The hypothesis that the differential response of the body tissues to nutrition is dependent upon their differential rates of growth is fully confirmed by the data. We see this not only in the relatively greater effect upon late-developing parts than early of both High and Low levels, but also in the increased competitive capacity of late-developing units for nutrition with increased age.

The concept of the shape of the growth curve as a factor of importance

in the development of the animal is a relatively new one. Dunlop & Hammond (1937) first suggested its significance in studying the growth and proportions of the rabbit's ear (early-developing part) in relation to body weight (late-developing part). Sufficient evidence has been produced to emphasize its implications to the breeder and feeder of pigs. That it is no less significant in the production of other animals is implicit in its differential growth basis. Its relationships in this connexion will be dealt with in Part V. In respect to the general field of application it is important to emphasize that the changes induced by control of the shape of the curve are comparable in nature and basis to the evolutionary changes which have occurred in the development of a breed. Breed improvement has consisted in advancing the relative development of late-developing characters. Application of the principles emerging from this study must recognize this; the fact that different breeds and strains within a breed vary in their rate of maturity will affect the extent of the response to differences in the nutritional environment of the type we have employed. For example, if it is required to reduce the growth of fat in the production of a bacon pig from an earlier maturing breed or type than the animals we have employed, the rate of growth would need to be reduced either earlier or to a greater degree than has been the case in this study.

To the animal nutritionalist no less than to the practical breeder and feeder, appreciation of the influence of the shape of the growth curve of the animal is essential to the interpretation of the effects of nutritional treatments. Animals on the same rations—and not necessarily due to genetic differences to which variations are usually attributed—invariably grow at different rates. These differences are frequently of considerable magnitude and will be responsible for variations in carcass proportions and composition.

It is to be emphasized that at 200 lb. live weight the pig is still relatively immature. Weights of 500–600 lb. are frequent in the Large White breed. Of considerable scientific and practical interest, therefore, is the question of the permanence of the effects that have been produced. From the relative effect on the early-developing skeletal units of the pigs underfed throughout we have seen that in these older animals there is some suggestion of a permanent effect. The position is somewhat obscured by the fact that these animals had absolutely the larger bones. It would be of interest to know what size would be attained by the skeleton of the pigs on a High Plane throughout if this treatment be continued until the animals attain the same age as the Low-Low at 200 lb. An experi-

ment in this direction is in progress, and from the appearance of the live animal it is evident that a far greater skeletal size has been attained. In respect to other species the evidence is somewhat conflicting in respect to the permanency of the effects of under-nutrition. The steers of Waters (1910) were not stunted in their maturity size, while Eckles and Swett (1918) report similar results with heifers. In both these cases under-nutrition did not commence until a relatively advanced stage of life. From our results it would appear that the earlier in life underfeeding is operative the greater the effect. In rats, Osborne & Mendel (1914-16) report a series of investigations in which resumption of growth to normal maturity size followed initial and long-period underfeeding. Many of their attempts at complete recovery failed however. On the other hand, Aron (1911) with dogs, Jackson & Stewart (1920), McCay et al. (1934), Conte-Marotta (1937) and Jackson (1937) with rats, all produced permanent effects upon maturity size when under-nourishment began soon after birth. In all cases, however, marked recovery followed better feeding. Walton & Hammond (1938) obtained a permanent effect upon maturity size in the horse which they attribute to differences in the level of nutrition during the pre-natal and pre-weaning stage. To students of human development the evidence afforded of the remarkable capacity of all tissues for recovery from the effects of relatively long-continued under-nourishment will be of considerable interest. Capon (1937) attributes the increased weight and height attained by substandard army recruits after a short period of good nutrition and exercise to the complementary effect of these two factors. Our evidence of the effect of nutrition alone in stimulating the growth of bone and muscle is of importance in this connexion.

From the animal production point of view it is very desirable that an experiment with the larger animals and similar in design to the present study be carried to the maturity stage. At the moment all we can say is that it seems highly probable that the nutritional environment can affect the maturity size and anatomical composition of the animal; that in general terms the degree of under (or ample) nutrition, the stage of development and the length of the period over which this is operative will be the determining factors.

(13) Summary

It is impracticable to give a detailed summary of the many findings of this experiment; attention is confined, therefore, to the major aspects and the general principles emerging.

1. By quantitative control of the plane of nutrition, twenty closely inbred pigs have been made to conform to four major variations in the shape of the growth curve from birth to 200 lb. live weight. A high rate throughout (High-High), a high followed by a low rate (High-Low), a low followed by a high rate (Low-High) and a low rate throughout the period (Low-Low) afforded comparison between animals of the same weight but different age and between animals of the same weight and age but with differently shaped growth curves. The relative effects of the treatments upon the development of body proportions and anatomical composition have been studied.

2. The results obtained afford convincing evidence of the influence of the nutritional environment as a directive and controlling force in the development of the animal body.

3. In body form two distinct types of pig were produced; the High-High and Low-High pigs were similar with a greater proportionate development of the late-developing parts of the body. Compared with these, the High-Low and the Low-Low showed proportionately greater development of the early-developing parts. Within each type the animals subjected to inadequate nutrition in early life showed the effects noted to a relatively greater extent.

4. Even more striking and statistically significant effects were produced on the major body tissues. The amount of skeleton and muscle increased and fat decreased in the treatment Low-High, High-High, High-Low, and Low-Low. Mean treatment differences relative to Low-Low ranged from 6 to 20% less in bone, 5 to 25% less in muscle, and 26 to 64% more in fat.

5. As at 16 weeks, the organs as a whole exhibited a relatively high degree of resistance to varying nutritive planes, but individual units showed well-defined and significant differential effects. A functional basis provides an adequate explanation of the facts. Under a limited nutritive supply growth gives way to function, and under an ample supply these organs whose functions are more directly associated with growth benefit relatively more.

6. The results fully support the hypothesis advanced in explanation of the effect of high and low nutrition up to 16 weeks upon the development of the body. Tissue response is differential and closely dependent upon the differential rates of growth of the different tissues. Earlier developing tissues are able to compete more efficiently than late for inadequate nutrition; the growth of late-developing parts is encouraged by ample supplies. The present experiment permits an extension of this

view in indicating that as growth proceeds the competitive capacity of late-developing tissues increases even under continued undernourishment. This is due to the proportionately greater decline in the growth intensity with age of the earlier developing parts. The period of life (stage of development) over which the nutritional environment is varied thus affects the nature of the response.

7. All tissues show remarkable recuperative capacity on provision of ample nutritive supplies following undernourishment. In line with the explanation above, this is relatively greater in respect to late-developing tissues than early. For this reason the "time factor" is important in affecting the absolute extent of the recovery made. Alteration in the absolute rate of growth of any tissue by nutrition cannot exceed a maximum.

8. As between the tissues, so within the anatomical units of each, marked differential effects were produced. In the relatively resistant skeleton these were apparent in both weight and form, and are capable of explanation along the lines noted above; i.e. on a basis of the differential growth relationships existing between the skeleton and other tissues on the one hand, and between the various skeletal units on the other. The response of both muscle and fat in different regions of the body similarly falls within the limits of this hypothesis.

9. Histological examination of the muscle shows that the weight response of this tissue to nutrition is closely associated with the size of the muscle fibre. Chemical data on muscle and fat tissue support the general thesis of the nature of tissue response to nutrition.

10. The sexes differ markedly in their anatomical composition, hogs being characterized by less bone and muscle and more fat than gilts. The extent of the difference can be modified by the rate of growth (plane of nutrition) imposed.

ADDENDUM TO PART III

Arising out of the results of the experiment reported in the foregoing, a further experiment was designed to investigate the effect upon body development of qualitative differences in the plane of protein nutrition in conjunction with differences in the shape of the growth curve. We have been interested here in determining whether our contention that the results obtained by quantitative control of the shape of the growth curve are applicable in principle to one of the major qualitative variations in nutritional practice. There was the further and equally important

reason that of the marked recuperative capacity of muscle tissue exhibited in the high-protein series might have been associated with the high level of protein of the ration. While the relationship of muscle development to protein is somewhat in dispute between workers, sufficient evidence was available to suggest this as a possibility. In designing this experiment we were particularly interested to see whether the pigs on a low level of nutrition from birth that showed a 300% deficiency in muscle weight at 16 weeks, and that under a High Plane of protein nutrition largely made up this deficit at 200 lb. live weight, could do so on a Low Plane of protein feeding. Because of the influence of the shape of the curve it was considered essential to maintain a difference similar to those of the first series. The experiment thus has the additional function of testing the validity of the result of that series.
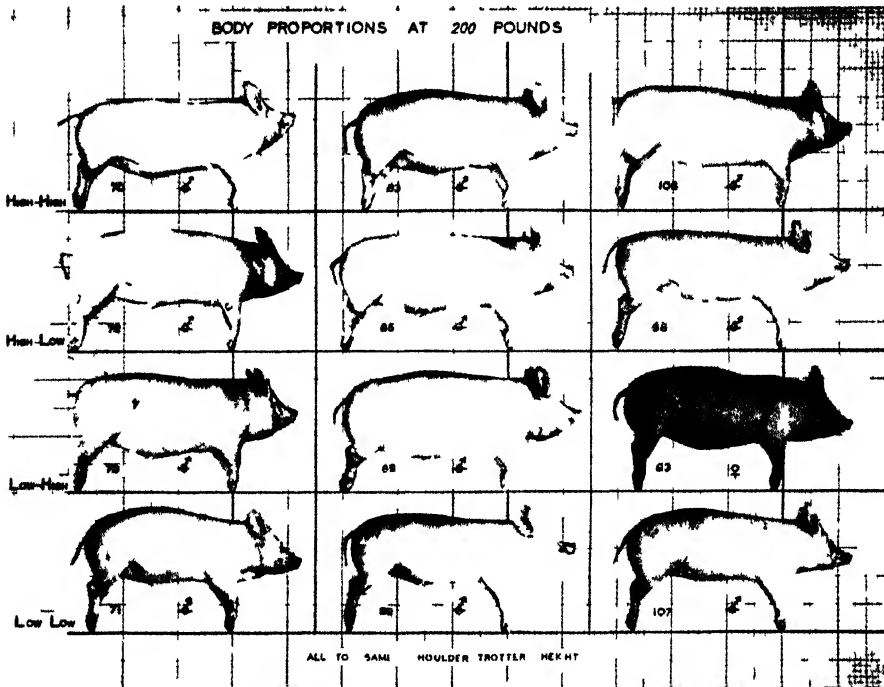
The experiment of Part III was thus repeated in precisely the same form up to 16 weeks; from this stage the pigs on each curve were placed on a ration containing only a 4% addition of separated milk powder as protein concentrate to a pure grain ration, as compared with 30% of fish meal plus raw separated milk of the first series. Similar quantitative control was effected and the same types of growth curve followed. Five sets of four pigs were again employed.

The last animal of the series has recently been slaughtered, and while the results have not been subjected to detailed analysis, it is possible to indicate the general nature of the results. These may be summarized very briefly as follows:
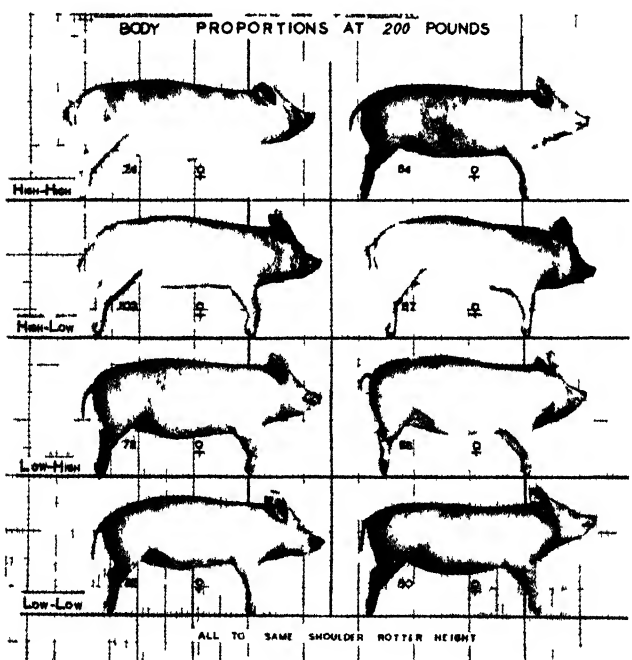
(1) The High-High pigs averaged 144 days, High-Low and Low-High 294 days, and the Low-Low 320 days at 200 lb. Growth on the low-protein ration was thus as rapid as on the high.

(2) The alteration in the protein level, well below that employed in normal practice, produced no noticeable diminution in the capacity of muscle to recover from initial retardance. This result may be attributed to the fact that though the percentage protein in the ration was low, the gross daily intake of food to allow for the rapid growth attained was such that the protein intake was sufficient. Similarly, in the Low-Low pigs, the daily growth rate was so low that even the low-protein intake was sufficient for muscle growth made under such conditions.
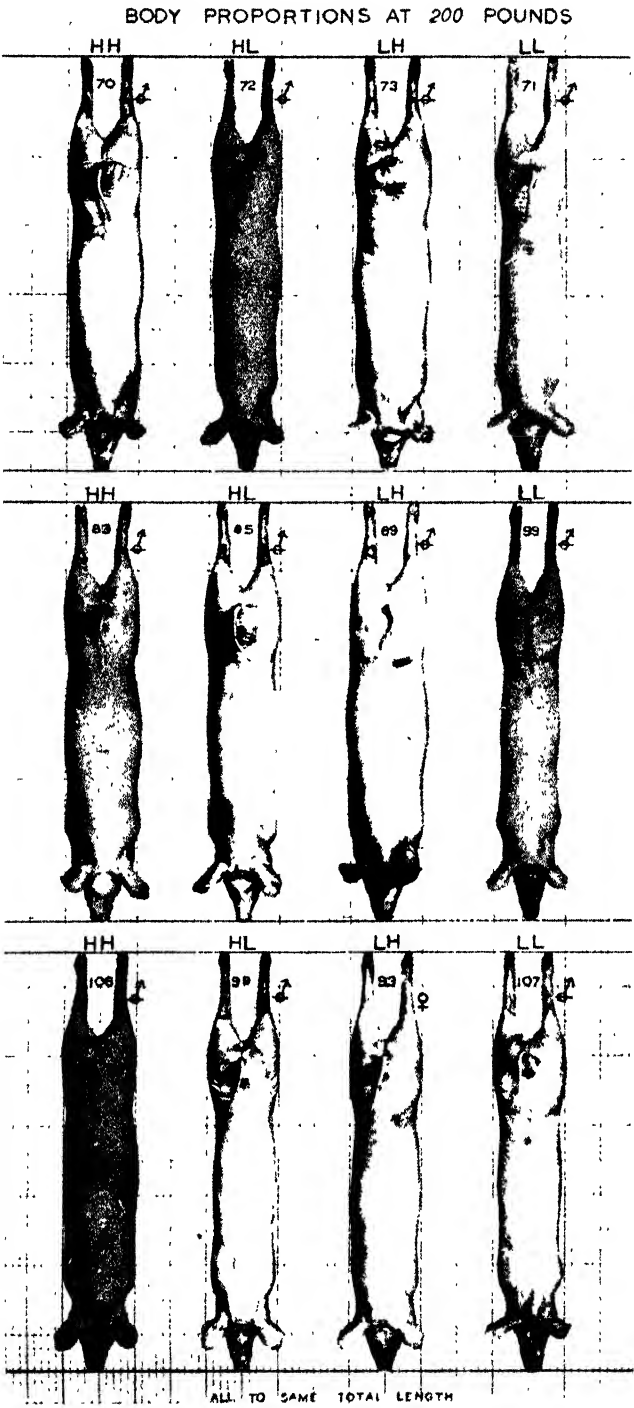
(3) No noticeable effects were produced upon the fat content of the carcasses; this is in line with the absence of effect upon muscle and contrary to the generally accepted opinion that a low-protein ration encourages fat and retards muscle growth. The results support fully those of Woodman *et al.* (1936) in this connexion.
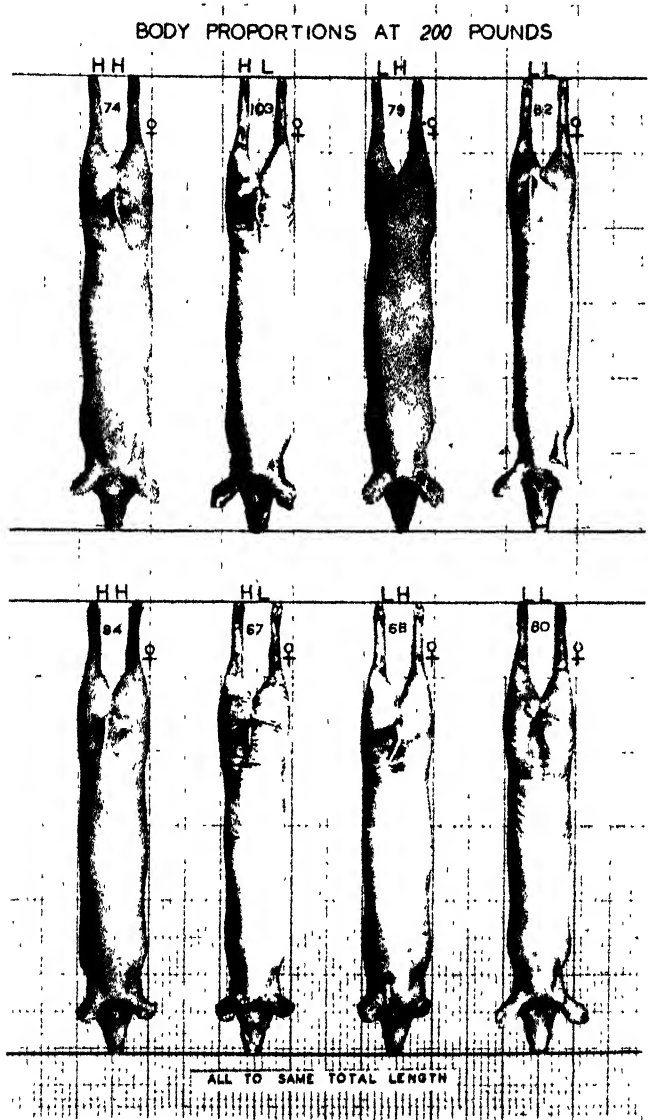
Hogs

Gilts.

BODY   PROPORTIONS   AT   *200*   POUNDS

Hogs.

Gilts.

PLANE OF NUTRITION ON KIDNEYS AT 200 POUNDS

ALL TO SAME SCALE

HIGH–HIGH

HIGH–LOW
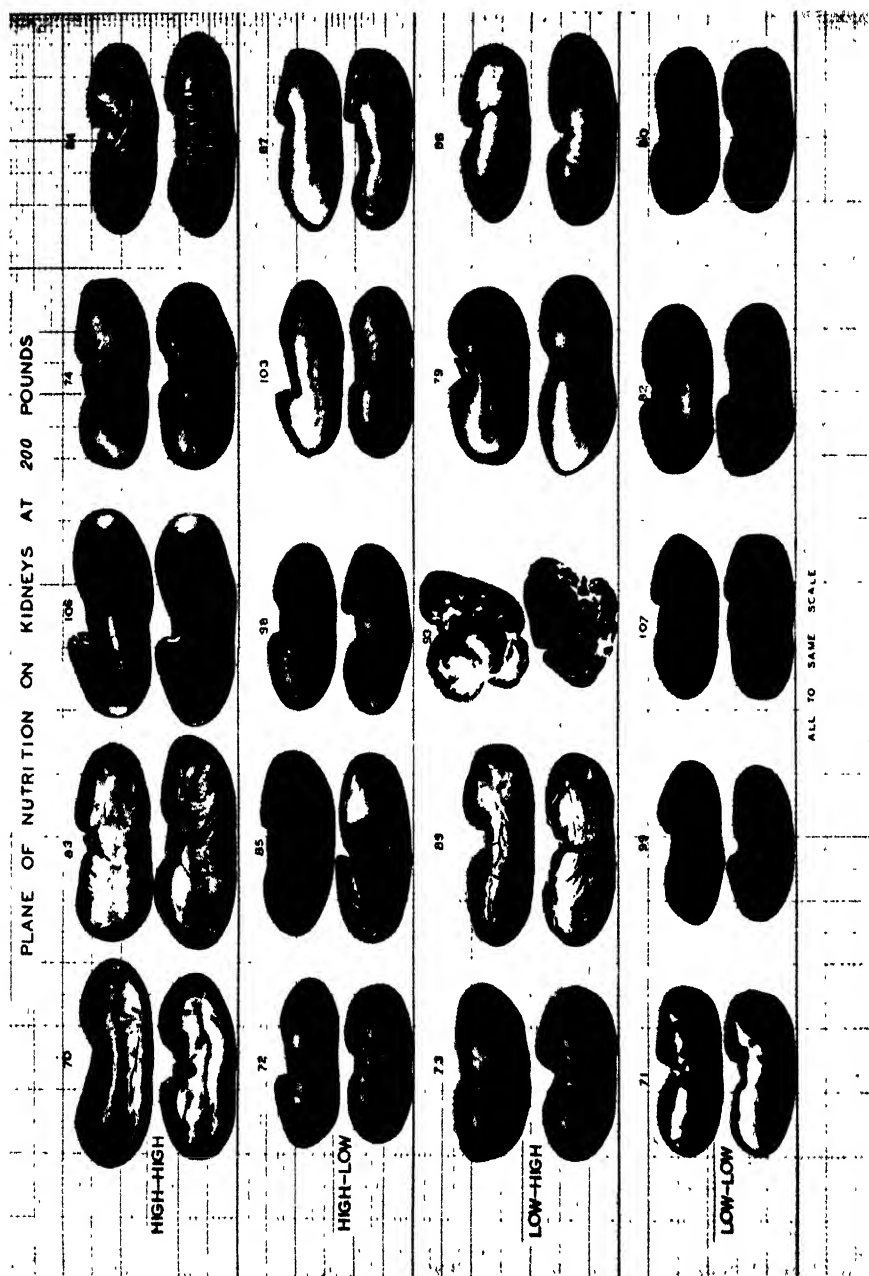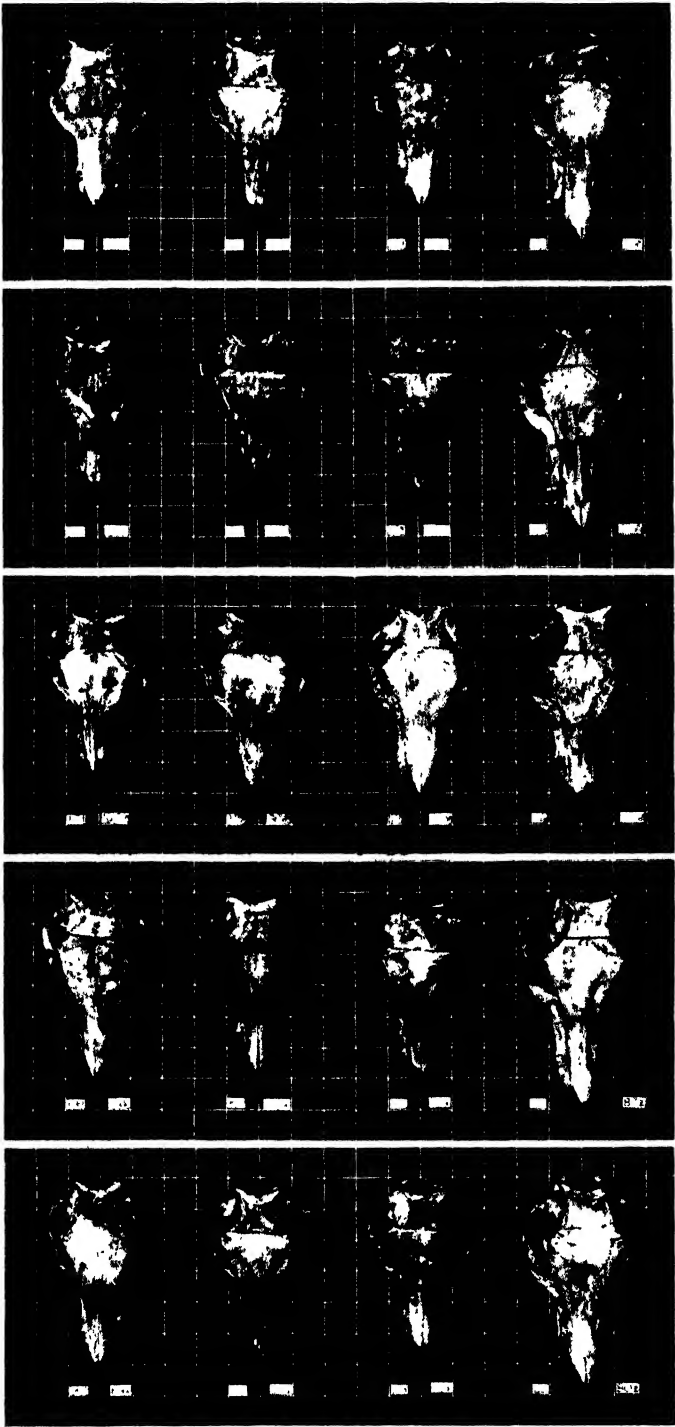
LOW–HIGH

LOW–LOW

Skulls.
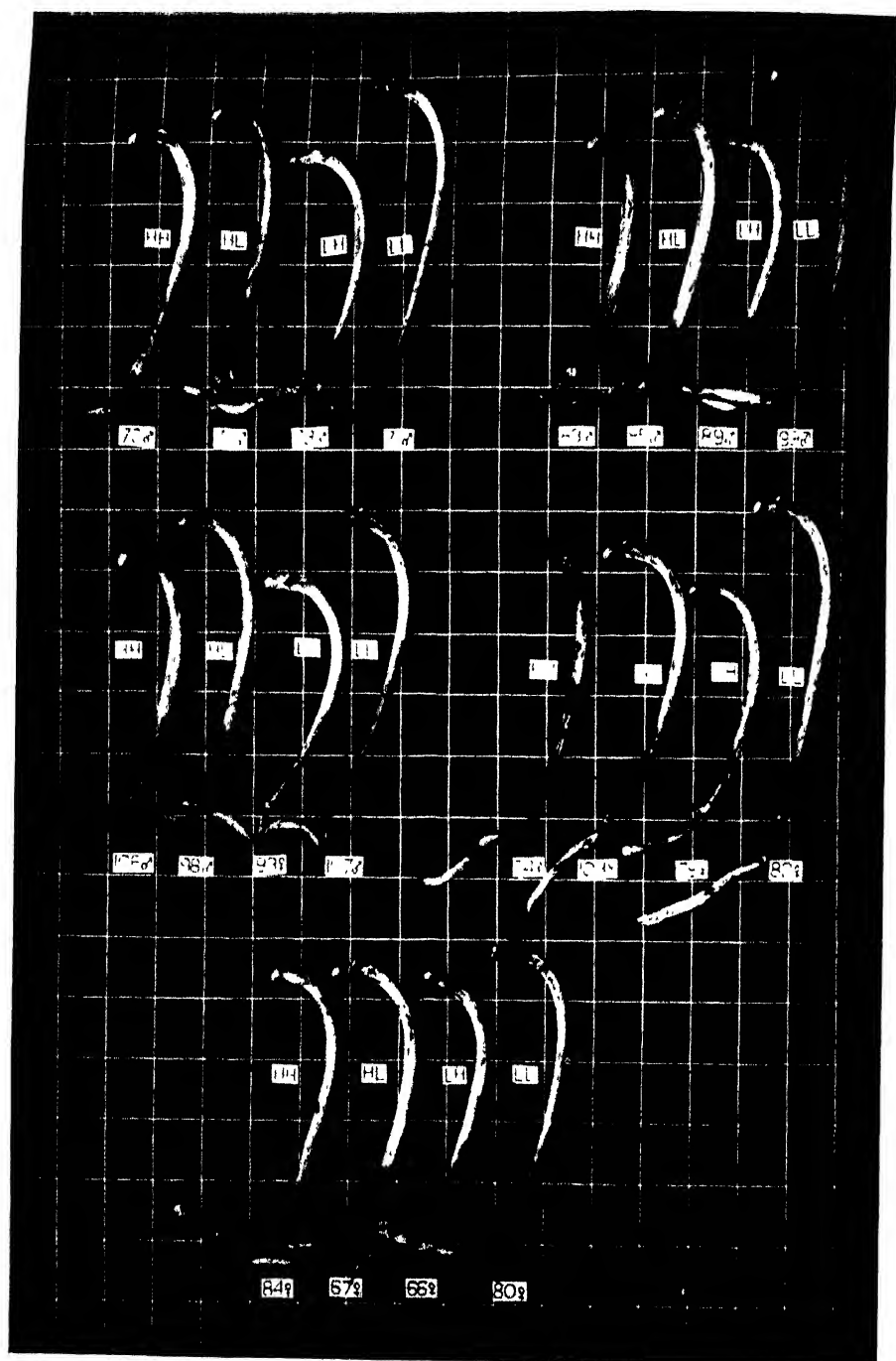
Sixth rib.
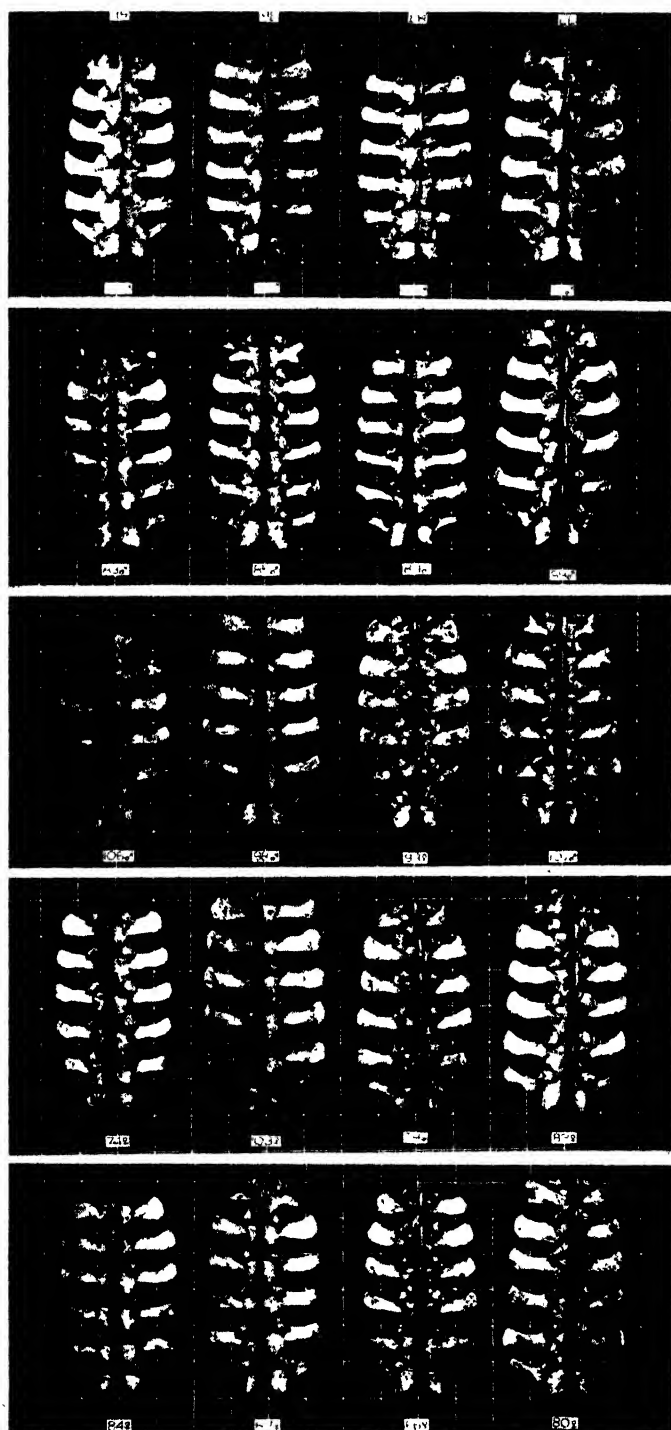
Lumbar vertebrae.
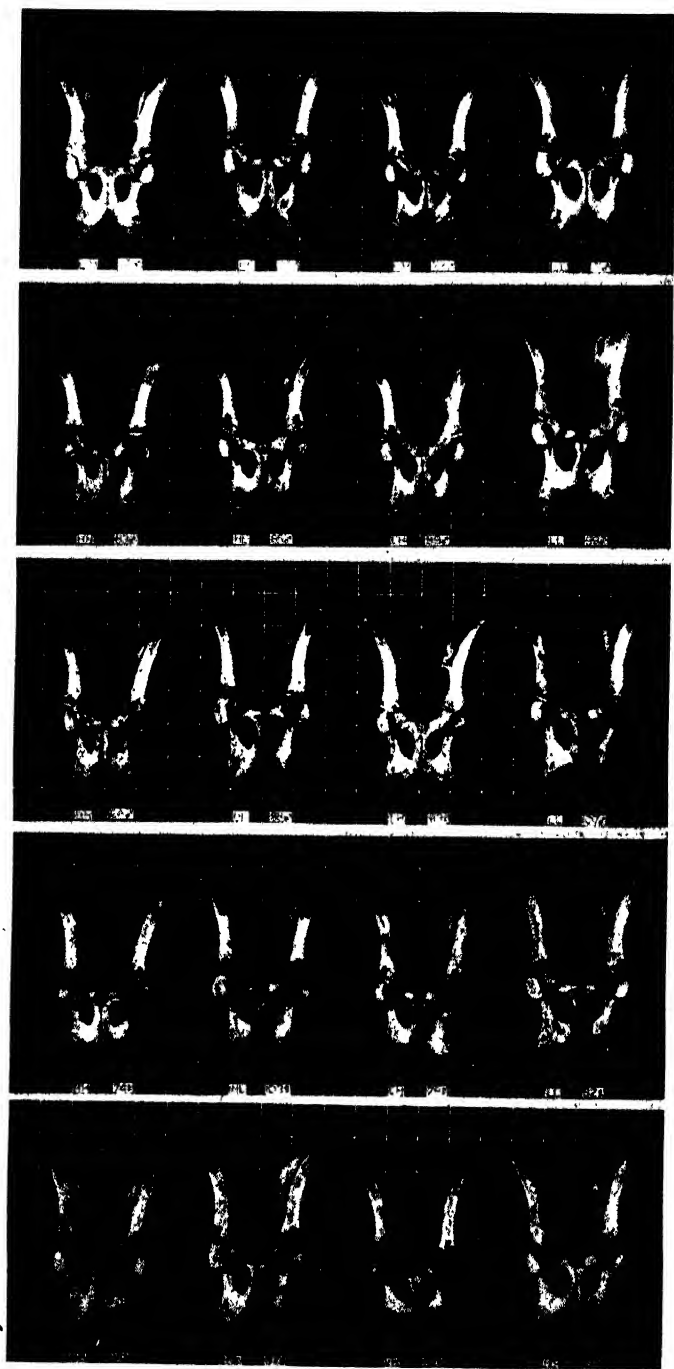
Pelvis.
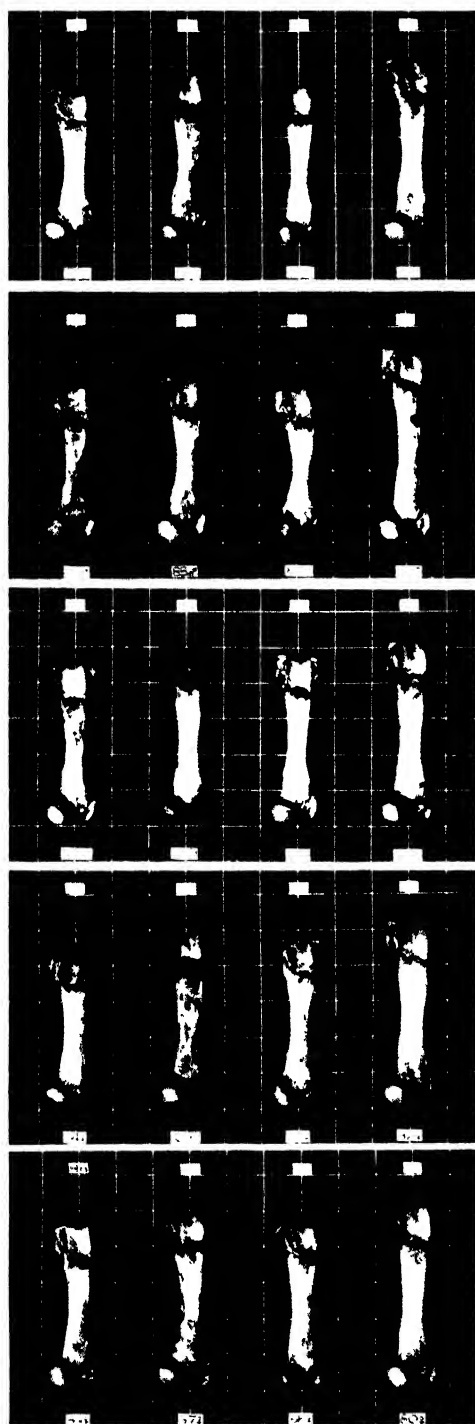
Femurs.
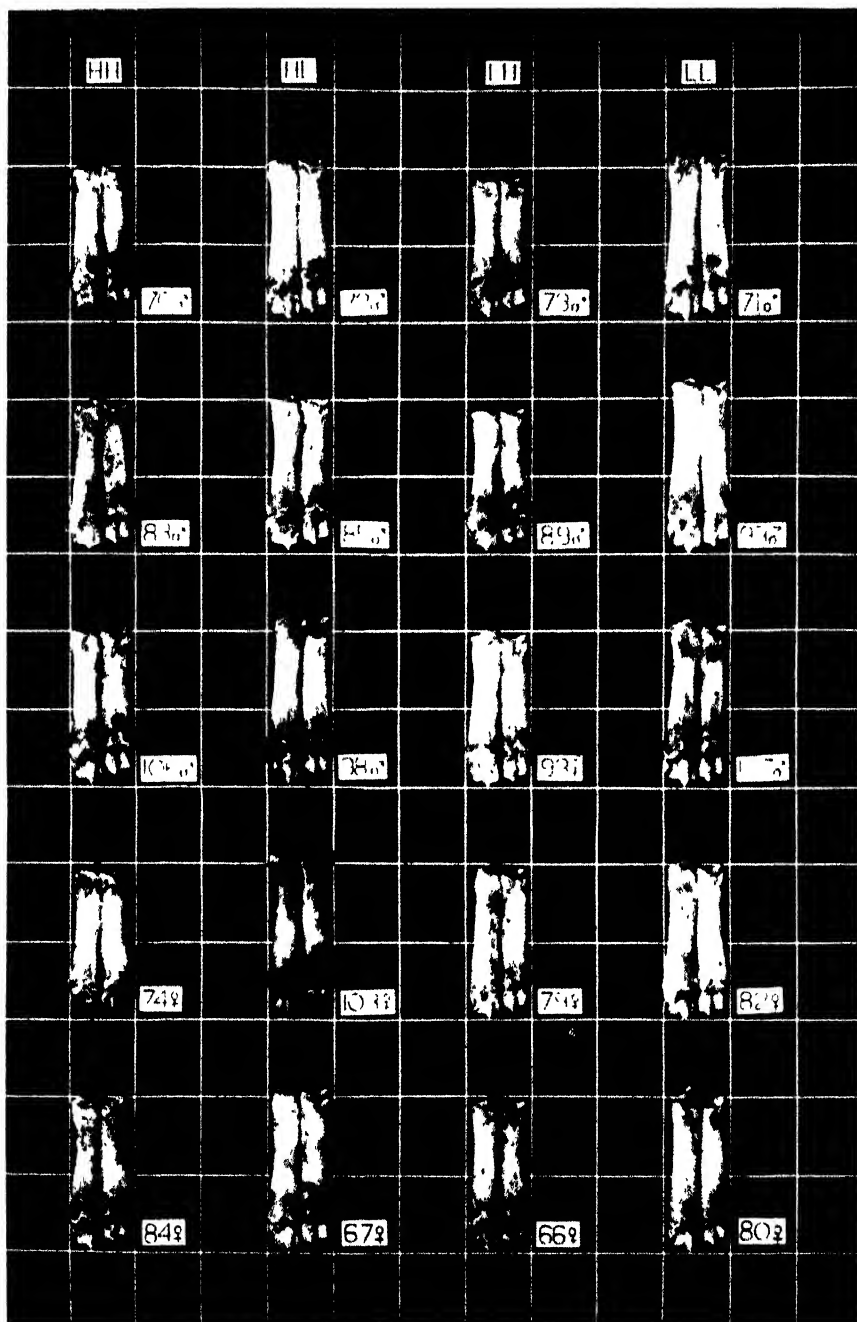
Hind cannons (metatarsals).
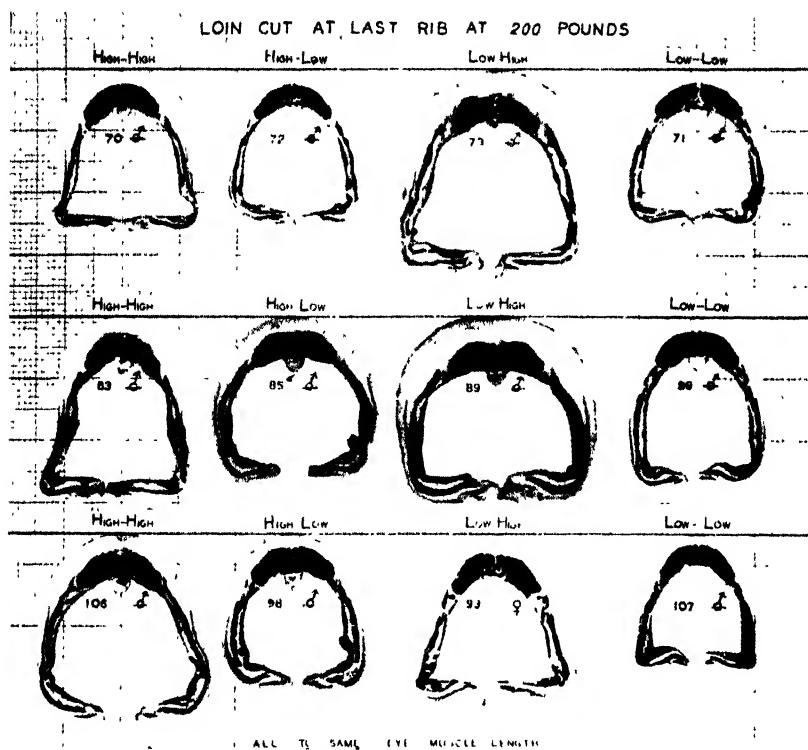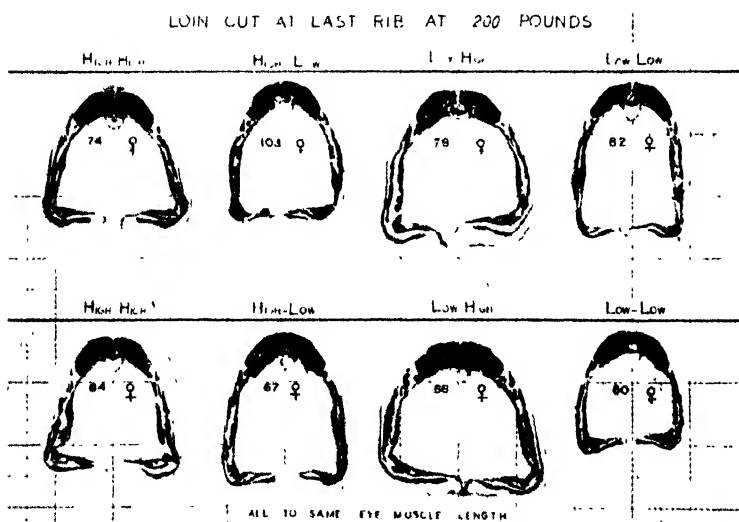
LOIN CUT AT LAST RIB AT 200 POUNDS

A. Hogs

LOIN CUT AT LAST RIB AT 200 POUNDS

B. Gilts.
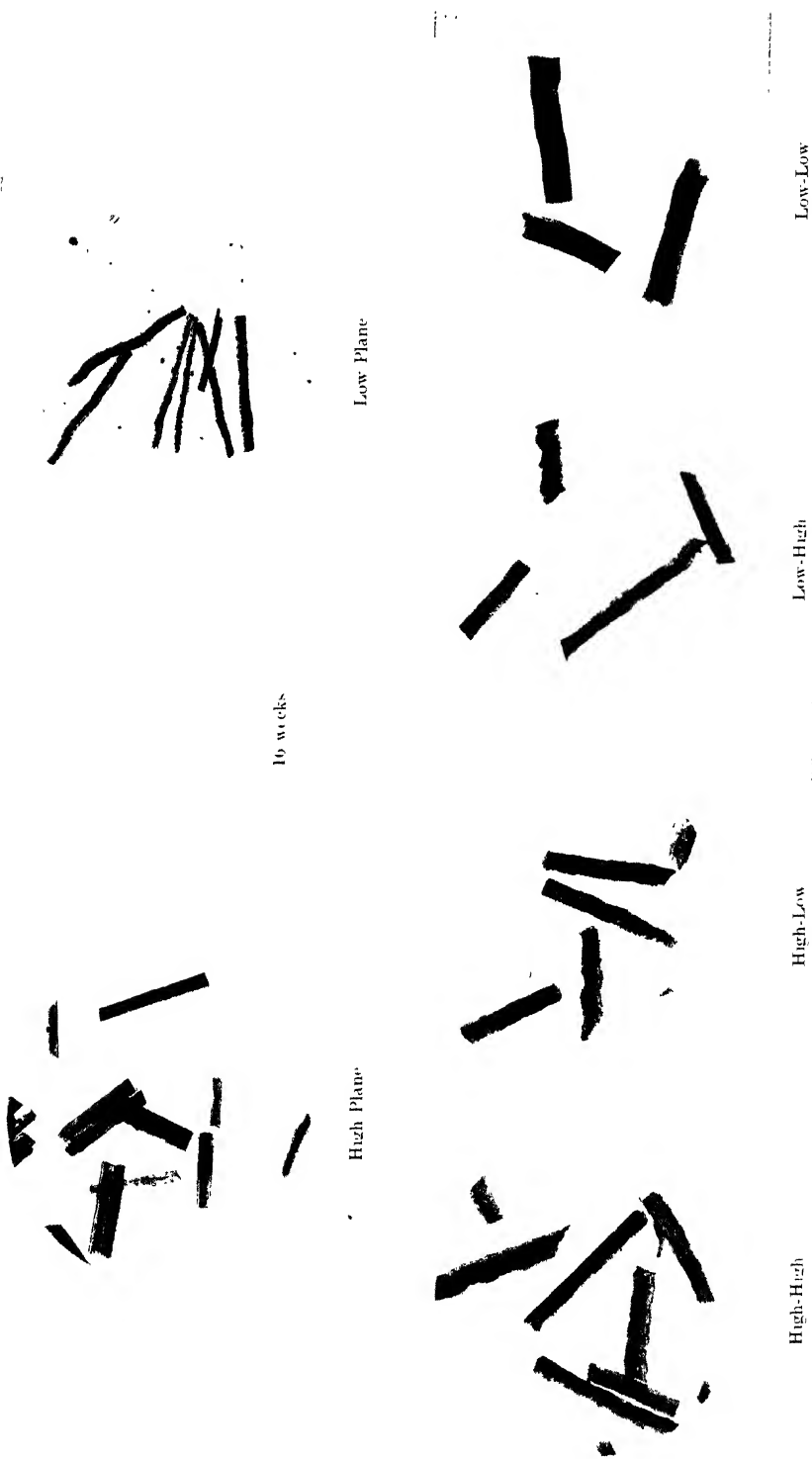
Effect of plane of nutrition on size of muscle fibre (longissimus dorsi). Magnification . 100.

Low Plane

16 weeks

High Plane
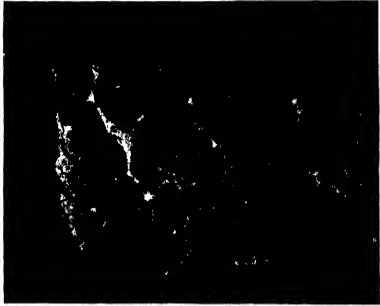
Low-Low

Low-High

High-Low

High-High
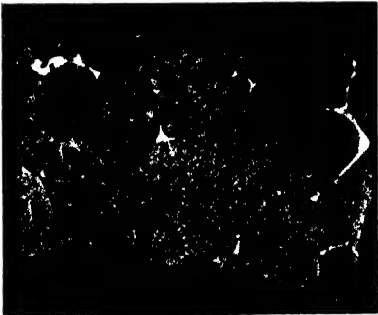
200 pounds

Influence of plane of nutrition on intra-muscular fat (marbling fat). Magnification × 3.
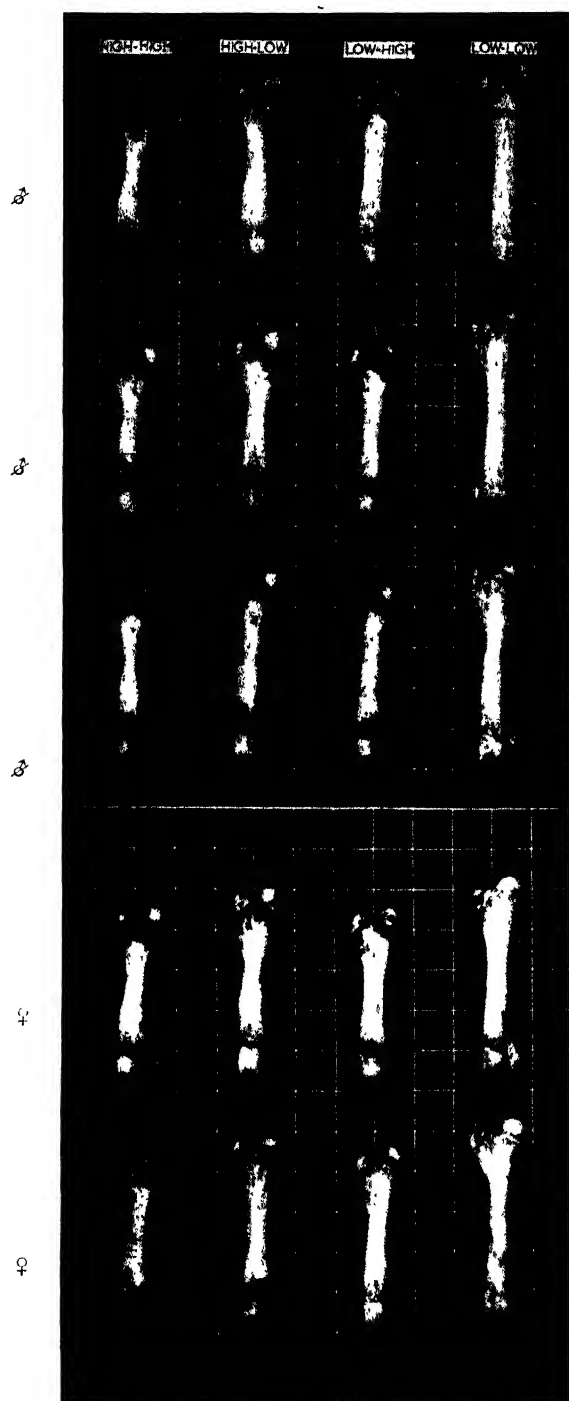
Femurs. Low protein series; compare with Pl. 25.

(4) The treatment differences were similar in nature and degree to those of the first experiment. Bone and muscle increased and fat decreased in the treatment order Low-High, High-High, High-Low and Low-Low. The experiment thus provided very strong support for our emphasis upon the shape of the growth curve as a major factor in the development in body proportions and anatomical composition of the animal.

(5) The close agreement with the results of the high-protein series can be observed in the effect upon the femur shown in Pl. 30.

(To be continued)

GAS AND VAPOUR MOVEMENTS IN THE SOIL

II. THE DIFFUSION OF CARBON DIOXIDE
THROUGH POROUS SOLIDS

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(With Two Text-figures)

In the first paper of this series (Penman, 1940; referred to below as I) it was suggested that the low values reported by Buckingham (1904) for the diffusion of carbon dioxide through soils could be attributed to his premature observation of the diffusion rates, the disturbing factor being the adsorption of gas by the soil, which retards the attainment of the steady state. Evidence of retardation was obtained in the experiments with carbon disulphide and acetone (I), and the work of Smith & Brown (1933), discussed below, provides indirect evidence of the same effect for carbon dioxide diffusing through soils. The simple and accurate technique devised for the vapours of carbon disulphide and acetone will not serve for experiments with carbon dioxide, but because of its great biological importance an attempt has been made to overcome the experimental difficulties disclosed by the results of earlier workers, and to obtain quantitative confirmation of the explanation advanced by the author to account for the discrepancy.

Buckingham's chief trouble was to produce and maintain a known partial pressure gradient across his soil samples without causing any difference in total pressure, and he expressed doubts as to whether his technique was always satisfactory. In the course of an attempt to improve on Buckingham's arrangement, Smith & Brown found that their soil samples were biologically active and producing carbon dioxide. In calculating diffusion coefficients a correction was made for the soil-produced carbon dioxide, but as far as it is possible to recalculate their results from the data supplied, the coefficients tabled appear to be too small ($c. \times 1/30$), suggesting some systematic arithmetical error in their calculations. Because of this and the need for a correction factor the numerical values of their coefficients will not be discussed, but attention is directed to one general feature of the results. "The rate of diffusion

increased with the length of the diffusion time in all cases except one.... Thus it would seem that the correction factor was inadequate."

This explanation is probably only partly true, and it is almost certain that Smith & Brown were getting experimental evidence of a source of error unsuspected by Buckingham, namely, adsorption of the gas by the soil. It is therefore obvious that the general nature of these results reinforces the conclusion already reached, viz. that for reliable measurements of the steady state dependence of diffusion upon porosity it is necessary to eliminate the effects of adsorption, either by using non-adsorbing materials or by delaying observations until the adsorption is complete. To avoid corrections for biological activity the granular materials must be biologically inert, and we must therefore avoid the use of soils when working with carbon dioxide. This is not a serious restriction, for we have seen that moist and dry soils conform to the general behaviour of other solids when carbon disulphide and acetone are used, and we assume that the same will be true for carbon dioxide.

A method of producing a partial pressure gradient of carbon dioxide has been devised and is described below. It is believed that it satisfies the condition that there must be no total pressure gradient, i.e. no viscous flow of an air-CO_2 mixture, but it suffers from one disadvantage. It is not possible to make a determination of the coefficient of diffusion of carbon dioxide into free air (D_0), and the value used in the calculations is $D_0 = 0.139$ cm.^{2}/sec. This is the mean of a number of values taken from standard works of reference, the individual values ranging from 0.134 to 0.142 cm.^{2}/sec.

THE APPARATUS AND METHOD OF OPERATION

The apparatus is conveniently described in three sections: (i) the reservoir, (ii) the diffusion apparatus, (iii) the measuring system.

(i) *The reservoir.* Instead of using Buckingham's method of producing a gas mixture by mixing streams from cylinders an automatic method has been used, based on the dissociation of sodium bicarbonate in solution. This proceeds until an equilibrium is set up between the concentrations of carbonate ion and dissolved carbon dioxide, the latter coming into equilibrium with the carbon dioxide content of the air above the solution. Ten litres of solution containing sodium carbonate (c. $M/10$) and sodium bicarbonate (c. $M/2$) were made up. In a closed system the air above the solution gradually attains an equilibrium, the carbon dioxide content being about $1\frac{1}{2}$% (by volume) at 25° C. The solution is

kept in two graduated 10 l. jars and, at the beginning of an experiment, one, the reservoir, will contain about $1\frac{1}{2}$ l. of solution. The air above this solution, presumed in equilibrium, can be displaced by running in liquid from the second jar, a delivery tube carrying the displaced mixture to the diffusion apparatus. About 7 l. are run in, thus leaving $1\frac{1}{2}$ l. in the second jar which then acts as the reservoir in the next experiment. A reservoir thus provides about 7 l. of a mixture of carbon dioxide and air for each experiment, and under the restricted conditions this is sufficient. The attainment of equilibrium is rather slow, and this simplified system has been slightly modified by introducing a third jar and a further 2 l. of solution, and limiting experiments to two per day, after which the jars are left overnight to come into equilibrium.

(ii) *The diffusion apparatus* (Fig. 1). The cylindrical holder previously employed is screwed into the tray of a tobacco tin which fits easily over the rim of a wide-necked bottle cut in half, a rubber gasket at the holder-tray junction and a rubber band at the tray-bottle junction making the joints gas-tight. Supported over the holder is a cylindrical collecting chamber with a clearance of 2 or 3 mm. at the bottom, sides and top. From the centre of the top of this chamber a tube leads away to the measuring system, and a side limb leads to an oil manometer. An aspirator behind the measuring system draws air up the sides of the holder and across the top of the granular solid in it, and any gas which diffuses through the solid from below is carried away in this air stream. To remove the normally occurring carbon dioxide from the air before it enters the collecting chamber, the upper part of the apparatus is loosely surrounded by a packing of Sofnolite (soda-lime + indicator). Blank experiments showed this to be quite efficient at normal rates of flow without causing any reduction of total pressure at the surface of the sample in the holder. Cleaning of the air in this or some other way is essential, as local variations in carbon dioxide content are sufficiently great to prevent reproducible results being obtained.

The space below the holder is closed by a rubber stopper carrying three tubes. The central one is connected to the delivery tube of the reservoir, and opens out conically to within about 1 cm. of the grid at the bottom of the holder. In this way the velocity of the gas-air mixture is reduced to negligible proportions and the incoming mixture is uniformly distributed below the grid. The second tube is a wide outlet tube (diameter $1\frac{1}{2}$ cm.) which carries away the gas mixture without any increase of total pressure in the bottle. A little Sofnolite in this tube takes out most of the carbon dioxide before the stream passes out into the

atmosphere. A thermometer in the outlet tube records the gas temperature. The remaining tube is connected to the other limb of the manometer.

With this design of apparatus, the manometer shows that there is no excess of total pressure below, and no deficit above the holder except at
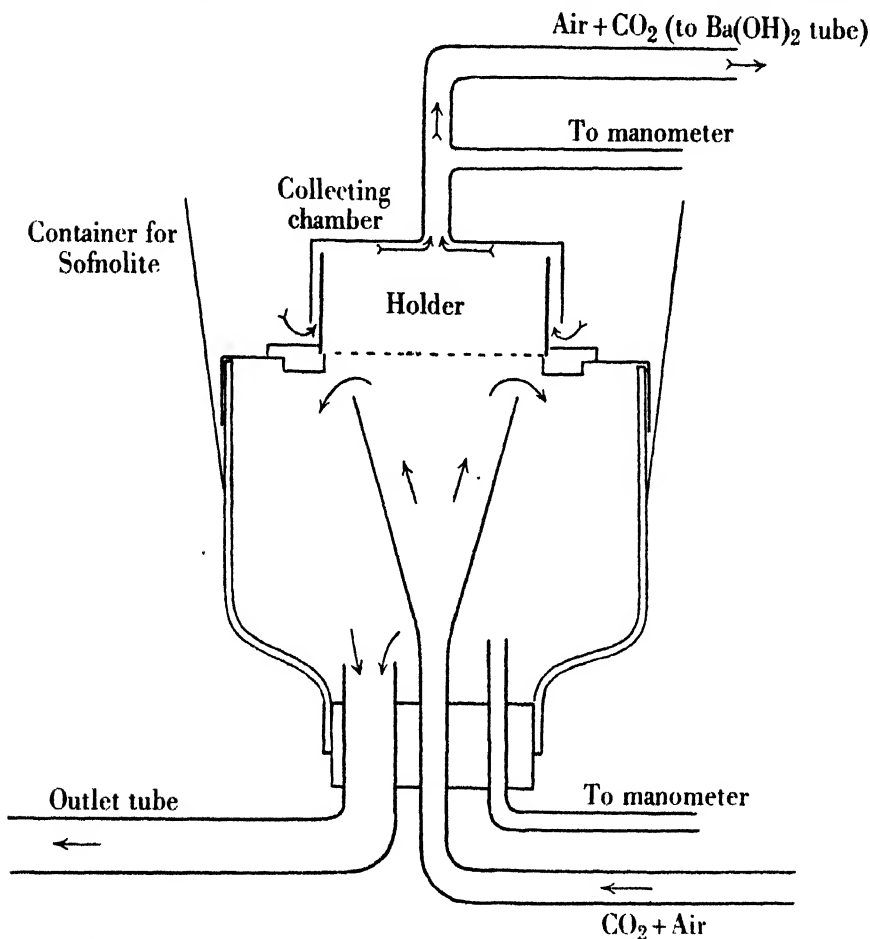
Fig. 1. Section of diffusion apparatus. (For the sake of clearness neither the granular solid nor the Sofnolite air filter is indicated.)

the instants of turning on the reservoir or aspirator taps. As a confirmation of the efficiency of the arrangement, results have been unaffected by changing the rates of flow.

(iii) *The measuring system*. The volume of air drawn through the diffusion apparatus is measured by the graduated aspirator. The air passes through one of two Pettenkofer tubes containing a measured volume of a solution of barium hydroxide and barium chloride. (The

stock baryta solution is almost saturated—*c. N*/5—and 10 or 15 c.c. are diluted to about 80 c.c. with CO_2-free water in the Pettenkofer tube.) The carbon dioxide is estimated by titrating the unchanged baryta with standard acid (*c. N*/10).

The method of operation is as follows. The holder is packed with the granular solid (sands, common salt, kaolin and kieselguhr, and mixtures of these have been employed) and weighed, the porosity being determined as previously described (1, p. 449). It is then replaced on the bottle, the rubber band slipped over the joint, and then the collecting chamber is clamped in position. Round the bottle is placed a bottomless split cardboard carton held in place by a rubber band, and this is filled with Sofnolite up to the level of the top of the collecting vessel.

One of the Pettenkofer tubes is filled with water and the other with the diluted baryta solution together with a few drops of thymol blue as indicator. At zero time the clock, the flow from the reservoir and the flow to the aspirator are started, the latter passing through the water tube. These conditions are maintained for a period varying from 20 to 60 min., depending on previous experience (1) of the particular material in the holder; at the beginning the rates of flow are adjusted and thereafter are kept as constant as possible. When the steady state is presumed to have been set up, the aspirator flow is redirected through the baryta tube by a two-way tap. To ensure complete absorption of the carbon dioxide a considerable excess of baryta is used, and in the experiments to be reported below the amount unconverted into carbonate was rarely less than three-quarters. The flow through the baryta tube lasts for a period between 60 and 20 min., at the beginning and end of which the temperature, aspirator and reservoir readings are noted. The other Pettenkofer tube is then washed out and a measured volume of baryta run in, diluted as before, connected directly to the reservoir, and a known volume of gas-air mixture is passed slowly through the baryta. The contents of the tubes are transferred separately to a suitable flask and titrated with acid previously standardized in terms of the stock baryta. Knowledge of the absolute concentrations is not essential for the calculation of the diffusion coefficient. From the first baryta tube the amount of carbon dioxide which has diffused is found, and from the second the concentration of carbon dioxide in the gas-air mixture, both expressed in terms of cubic centimetres of acid. The concentration difference causing diffusion depends upon both amounts. The higher pressure is reduced by the diffusion through the solid, and the lower pressure is given sufficiently closely by the concentration of the stream to the aspirator.

Experimental results

The experimental data must be corrected for the impedance of the grid and of part of the air below to obtain the effect of the solid alone. Calculation of the uncorrected value of the diffusion coefficient is shown immediately below for a typical set of data and is followed by a consideration of the correction for the impedance of the grid and lower chamber.

Mixture of sand and kieselguhr ($S = 0.56$). Barometer: 29·8 in.

(i) Diffusion experiment.

> Mean temperature $= 22.5°$ C.
> Baryta in test tube $= 10.00$ c.c. $= 20.40$ c.c. HCl.
> Time: 40–70 min. $= 1800$ sec.
> HCl for unconverted baryta $\quad = 16.40$ c.c.
> $\quad\quad\quad \therefore CO_2$ diffused $= \overline{4.00}$ c.c. HCl.
>
> Volume from reservoir $= 2.57$ l.
> Volume to aspirator $= 3.25$ l.

(ii) Concentration experiment.

> Baryta in test tube $= 15.00$ c.c. $= 30.60$ c.c. HCl.
> Volume from reservoir $= 1.13$ l.
> HCl for unconverted baryta $\quad = 21.20$ c.c.
> $\quad\quad\quad \therefore CO_2$ absorbed $= \overline{9.40}$ c.c. HCl.

$\therefore$ Concentration air-CO_2 mixture $= 9.40/1.13$ c.c. HCl/l.
$\quad\quad\quad\quad\quad\quad\quad\quad\quad = 8.35$ c.c. HCl/l.

Mean concentration on upper side of holder $= 4.00/3.25$ c.c. HCl/l.
$\quad\quad\quad\quad\quad\quad\quad\quad\quad\quad\quad = 1.23$ c.c. HCl/l.

Mean concentration on lower side of holder $= 8.35 -$ (amount diffusing per litre)
$\quad\quad\quad\quad\quad\quad\quad\quad\quad\quad\quad = 8.35 - 4.00/2.57$ c.c. HCl/l.
$\quad\quad\quad\quad\quad\quad\quad\quad\quad\quad\quad = 6.79$ c.c. HCl/l.

$\therefore$ Concentration difference causing diffusion $= 6.79 - 1.23$ c.c. HCl/l.
$\quad\quad\quad\quad\quad\quad\quad\quad\quad\quad\quad\quad = 5.56$ c.c. HCl/l.

The coefficient of diffusion (D) is defined by

$$dq/dt = DA\,(n_2 - n_1)/l \quad \text{(I, p. 439),}$$

where $(n_2 - n_1)$, the concentration difference producing diffusion, is measured in units of q per c.c. In the above we take as our unit of quantity the carbon dioxide equivalent of 1 c.c. of acid. A and l are as before (22·30 cm.² and 2·64 cm.), and hence

$$D' = (4.00 \times 2.64)/(22.30 \times 5.56 \times 10^{-3} \times 1800)$$
$$= 0.0475.$$

This value has to be reduced to standard conditions ($T = 273°$ K. and $P = 30.0$ in.) and we obtain $D_{un} = 0.0405$.

Correction for impedance of gauze and lower chamber. In the earlier paper (I, p. 441) the diffusion current (C) was considered as dependent upon two factors, the diffusion potential difference (E) and the impedance

(Z) of the material through which the diffusion took place. The total impedance, $Z + Z_0$, was considered in two parts: one, Z, due to the material in the holder, given by l/DA, and the other, Z_0, including both the impedance of the gauze and of the air space between the bottom of the holder and the surface of the evaporating liquid. Using a fabric support on the grid the values of Z_0 were for carbon disulphide 0·78, and for acetone 0·88, the products $Z_0 D_0$ being 0·0803 and 0·0835 respectively, which should be the same for equal air columns beneath the holder. The mean value is 0·082, and the part contributed by the air column beneath the holder is given by the ratio of its depth to its area of cross-section. The reservoir used in I was 1·6 cm. deep, 34 cm.² cross-section, and with 7 c.c. liquid in it (0·2 cm. deep) the air column would be 1·4 cm. deep. Hence

$$D_0 Z_0 \text{ for the air column} = 1·4/34 = 0·041$$

and $\qquad D_0 Z_0$ for the gauze $\quad = 0·082 - 0·041 = 0·041.$

(The equality of these values is a coincidence.) This value will hold for the present apparatus, and to it must be added an amount depending on the position of the layer of the carbon dioxide-air mixture from which diffusion takes place (corresponding to the surface of the liquid in the earlier apparatus). The effective position of this layer lies somewhere between the bottom of the gauze and the top of the conical delivery tube, and we assume that it is midway between the two. The separation is 0·95 cm. and the area of cross-section of the bottle is 40 cm.², and hence the value of ZD for the space below the gauze is $0·475/40 = 0·0119$, and the total for air space and gauze is thus $0·0410 + 0·0119 = 0·0529$. Taking D_0 for carbon dioxide as 0·139 cm.²/sec., we obtain $Z_0 = 0·0529/0·139 = 0·381$. If Z is the impedance of the solid in the holder (for which $l/A = 0·1184$),

$$D = 0·1184/Z,$$
$$D_{\text{un.}} = 0·1184/Z + Z_0,$$
$$\therefore\ 1/D = 1/D_{\text{un.}} - Z_0/0·1184$$
$$= 1/D_{\text{un.}} - 3·21.$$

For the particular case for which $D_{\text{un.}} = 0·0405$,

$$1/D = 24·70 - 3·21 = 21·49,$$
$$\therefore\ D = 0·0465, \text{ i.e. } D/D_0 = 0·335.$$

If the layer of maximum concentration is assumed to be at the top of the conical tube or at the bottom of the gauze the value becomes 0·048 or 0·045.

The value of D may therefore be in error by $\pm 3\%$ at $S = 0·56$. The

possible error increases with S and will be $c. \pm 1.35\%$ at $S = 0.21$ and $\pm 5.6\%$ at $S = 0.87$. This source of error, if effective, will affect all results in the same sense; superimposed will be the random experimental errors arising from the measurement of volumes (reservoir and aspirator) and from the titrations (diffusion, concentration, and baryta-HCl check). As far as possible these have been eliminated by performing several experiments on each sample with different rates of flow and for different lengths
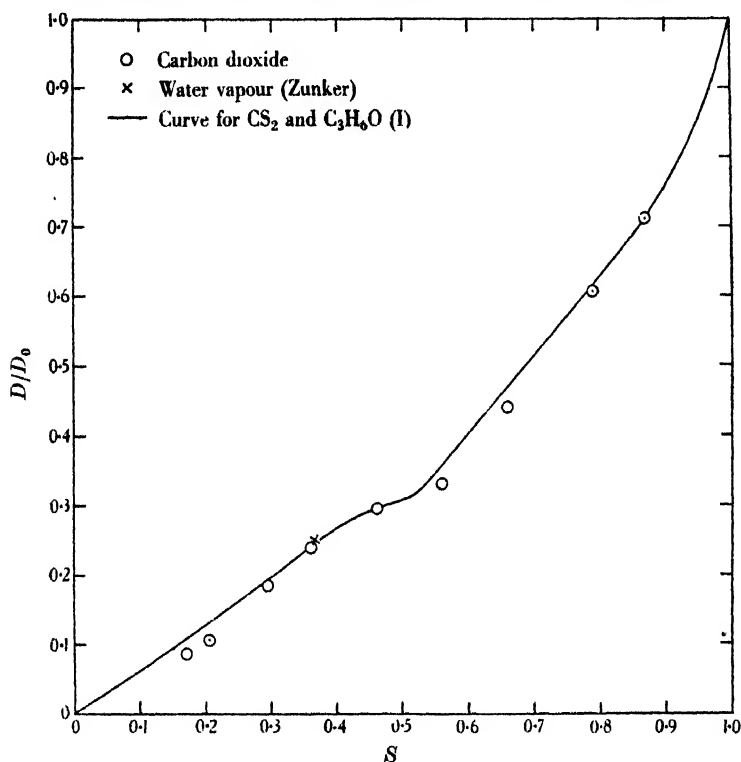
Fig. 2. Dependence of coefficient of diffusion on porosity

of time, and each point on the curve represents the mean of three or four determinations. The range of granular solids used is not as extensive as that used in I, and only those solids have been chosen which were known to come quickly to the steady state in the carbon disulphide experiments. In general, the sands were allowed about 20 min. to attain the steady state and the experimental run lasted for an hour, and for the more finely divided materials, such as kieselguhr and kaolin, the periods were reversed.

Sufficient experimental points have been obtained to permit a fair comparison of the results with those for carbon disulphide and acetone,

In Fig. 2 have been plotted the values of D/D_0, the curve obtained for carbon disulphide and acetone, and also an experimental point for the diffusion of water vapour. This has been calculated from the results, given by Zunker (1930), of experiments on the movement of water vapour through a column of sand. Although interpreted by Zunker in terms of viscous flow of the vapour, the conditions of the experiments were purely diffusive, and we may use the results to give an indication of the way in which water vapour conforms to the general behaviour.

<center>DISCUSSION OF RESULTS</center>

The points for carbon dioxide lie on or near the curve, and remembering that the present method of experiment cannot be as accurate as that used in I, which involved a weighing only, we conclude that the curve obtained for the vapours also holds for carbon dioxide diffusing through dry solids which are biologically inactive. In the experiments with carbon disulphide it was shown that moist and air-dry soils fitted into the same scheme, and it is reasonable to assume that in the steady state the diffusion of carbon dioxide through soils will depend upon the porosity in the same way, i.e. over the range of technical interest $(0 \cdot 0 < S < 0 \cdot 6)$, we may use the relation $D/D_0 = 0 \cdot 66 S$. In field soils it is exceedingly unlikely that a true steady state will ever be set up, because the centres of biological activity will, in general, be irregularly distributed in the soil and be of variable intensity, and the readjustment of partial pressure gradients will be retarded by the effects of soil moisture and adsorption in all soils, and also by chemical action in soils which contain an appreciable quantity of carbonate. The retardation will tend to smooth out the effects of small fluctuations in biological activity, but in the absence of direct knowledge of the nature of the adsorption equilibria between soil and gas one cannot say what is to be regarded as a "small" fluctuation. As long as the fluctuations are small a pseudo-steady state will be maintained; when the fluctuations are large the interpretation of the rates of surface emission of carbon dioxide in terms of soil activity will be very complex. The existence of large fluctuations may be the reason why some authors (e.g. Smith & Brown, 1931, 1932) have suggested that some other mechanism in addition to gaseous diffusion is needed to account for the irregular day to day variations in surface emission of carbon dioxide. To the complexity already noted there must be added the effects of changes in the environment. Changes in the porosity due to wetting or drying, and changes in the temperature of the soil, will modify the coefficient of diffusion; they will also modify the

gas-condensed phase equilibrium (using the term condensed phase to include dissolved, adsorbed and chemically bound gas), and it is therefore somewhat unreasonable to expect a simple diffusion theory to give an exact account of carbon dioxide movements in soil. The most that one can ask is that it should account broadly for the normal process of aeration. In the introductory survey of I we saw that even on the basis of Buckingham's equation the amount of diffusive flow was sufficient to account for normal aeration without invoking meteorological factors: the present account shows that his theoretical predictions were considerably underestimated.

As indicated in I, the materials to which this discussion is applicable are granular solids whose particles approximate to spheres and in which the distribution of pore space is isotropic. As the pore space in a soil is decreased by wetting, it is very probable that the isotropy will cease to exist; small air pockets may be formed which are completely isolated by liquid or solid from other parts of the soil atmosphere, and these will be ineffective as diffusion channels but still contribute to the pore space. It is to be expected, therefore, that the curve will become less reliable as the pore space decreases, and the backward extrapolation to $S = 0.00$ from $S = 0.15$ is to be regarded as indicating the order of magnitude of the diffusion coefficient. The actual value may be greater or less. It will be greater when the pore space is provided by vertical cracks in the soil, and will be less in cases where parts of the pore space do not contribute to the system of through air channels. This lack of precision in the application of diffusion theory to the aeration of wet soils will apply with equal force to any other mechanism which is postulated.

To make a quantitative survey of the effect of diffusion on aeration we make use of the relation $D/D_0 = 0.66S$, which was shown in I to represent the experimental results with sufficient accuracy over a considerable range of porosity. Let us assume that we have a uniform concentration gradient of carbon dioxide down to a depth of l cm., the concentrations (c.c./c.c.) being c_1 and c_2 at l and the surface respectively. Consider the emission of gas from an area A cm.^{2} of the soil surface, the porosity being S and the mean temperature $T°$ K. For the present purpose the pressure correction may be ignored. The volume of carbon dioxide passing out in time t (sec.) is given by

$$\Delta V \text{ (c.c.)} = t \times 0.66 D_0 S \, (T/273)^2 \times (c_1 - c_2)/l.$$

The total volume of carbon dioxide in the prism $(l \times A)$ is

$$V = lAS \times (c_1 + c_2)/2,$$

$$\therefore \ \Delta V/V = 1.32t \, D_0/l^2 \times (T/273)^2 \times (c_1 - c_2)/(c_1 + c_2).$$

As a first approximation, if c_2 is small compared with c_1, this becomes

$$\Delta V/V = 1\cdot32t\, D_0/l^2\,(T/273)^2,$$

which is independent of the concentration and the porosity. The significance of this equation is shown most conveniently by determining the time required to renew the air content of the soil, i.e. by setting $\Delta V/V = 1$ and finding t. Taking $T = 273 + 15$, and $D_0 = 0\cdot139$ cm.²/sec., we find $t = l^2 \times 1\cdot12 \times 10^{-3}$ hr. For $l = 30$ cm., $t \doteqdot 1$ hr., i.e. the air to a depth of 30 cm. will be completely renewed every hour. Where c_2 is not negligible, the period is increased by a factor $(c_1 + c_2)/(c_1 - c_2)$, and taking for illustration some data given by Russell (1937, p. 485) for arable land, (a) unmanured ($c_1 = 0\cdot2\,\%$, $c_2 = 0\cdot03\,\%$), and (b) dunged ($c_1 = 0\cdot4\,\%$, $c_2 = 0\cdot03\,\%$), the values of t become

$$t_a = 1\cdot35 \text{ hr.}; \quad t_b \doteqdot 1\cdot16 \text{ hr.}$$

For $l = 20$ cm., these values will be reduced to $4/9$ and t_a ($l = 20$) is $0\cdot60$ hr. This time may be compared with the finding of Romell, quoted by Russell (1937, p. 486), from which it was estimated that the soil air must be completely renewed every hour to a depth of 20 cm. to keep it at its normal composition. The times are of the same order, and we may summarize the effect of diffusion on aeration as follows. The physical conditions in the soil atmosphere are such that diffusion of carbon dioxide upward must be taking place and this movement may be accelerated by meteorological changes. The process of diffusion will be continuous, and in amount it is sufficient to account for the observed rates of soil respiration. Although an occasional favourable combination of meteorological changes may also be sufficient, such a combination is not a necessary condition for the promotion of aeration.

One further point remains to be discussed, bringing us back to one of the basic assumptions, namely, that the diffusion curve is unique. This *a priori* assumption has been confirmed for carbon disulphide, acetone and carbon dioxide, and a single point for water vapour conforms to the general behaviour. An application of this unique dependence of D/D_0 on S has been made (Penman & Schofield, 1939) to estimate the extent of water movement in soils as vapour under a vapour-pressure gradient arising from temperature differences. Even under conditions much more extreme than any likely to arise in practice, it was shown that the transfer was very small and that distillation under a temperature gradient is a negligible factor in soil water movements.

SUMMARY

Apparatus for measuring the rate of diffusion of carbon dioxide through granular solids is described and the results obtained with it are shown to conform to the curve connecting D/D_0 and S previously obtained for carbon disulphide and acetone. The equation $D/D_0 = 0.66S$, which it is suggested should replace Buckingham's equation $D/D_0 = S^2$, is applied to a discussion of soil aeration, and it is shown that at all porosities the rate of diffusion of carbon dioxide from the soil is sufficient to account for normal respiration without invoking the assistance of meteorological changes. A further application of the equation to water vapour movement in soils is briefly discussed.

REFERENCES

BUCKINGHAM, E. (1904). *Bull. U.S. Dep. Agric.* no. 25.

PENMAN. H. L. (1940). *J. agric. Sci.* **30**, 437.

PENMAN, H. L. & SCHOFIELD, R. K. (1939). Note submitted to the 7th General Assembly of the Intern. Union of Geodesy and Geophysics.

RUSSELL, E. J. (1937). *Soil Conditions and Plant Growth.* 7th ed. London.

SMITH, F. B. & BROWN, P. E. (1931). *J. Amer. Soc. Agron.* **23**, 909.

—— —— (1932). *J. Amer. Soc. Agron.* **24**, 577.

—— —— (1933). *Soil Sci.* **35**, 413.

ZUNKER, F. (1930). *Handbuch der Bodenlehre,* **6**, 202. Berlin.

GROWTH RATE AND CARCASS QUALITY IN BACON PIGS

A STUDY OF POLYNOMIAL COEFFICIENTS FITTED TO GROWTH RATE DATA

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(With One Text-figure)

RECENT experiments have shown that plane of nutrition exerts an influence on carcass quality (Mansfield *et al.* 1937; McMeekan & Hammond, 1939). It therefore becomes of importance to know how far carcass reports may be affected by variations in the growth rate of pigs arising under the customary pig-rearing conditions of the industry, whether they be due to temporary loss of appetite, to climatic or other environmental fluctuations, or to the action of differing gene combinations. Apart from the desirability of knowing to what extent carcass quality can be controlled after a pig is born, the need for improved methods of judging genotype from recorded measurements of carcasses requires that non-genetic variation should be carefully estimated and allowed for.

In a previous paper (Smith & Donald, 1939) the presence of extensive variation in the growth rate of pigs and whole litters during 28-day periods of their lives was discussed, and it was shown that under conditions of feeding which were as uniform as possible, without taking uneconomic precautions to control environment, the growth of litters in any period is not a reliable indication of subsequent performance. It follows that many litters growing comparatively quickly after weaning may be growing comparatively slowly in the later stages of fattening, and vice versa. The possibility that these facts concerning growth rate might be related to carcass quality has been studied in a group of forty-four animals all by the same boar, and farrowed within a fortnight (Donald, 1939). Since the sows were also interrelated, the genetic variance in these pigs should have been less than that obtaining in a random sample, and non-genetic variance therefore relatively more important. The variation in thickness of back fat and breadth of eye muscle, however, did not appear to be caused by differences in rate of growth as measured by increases in weight during various periods of the pigs' lives.

This study, being based on growth rates or gains calculated from initial and final differences in weight of a stated period, may have been hindered by some inaccuracy in estimating growth rate in this way. The work has therefore been extended to include the fitting of cubic curves to the data obtained from the fortnightly weighings during the growing period in the manner suggested by Wishart (1938, 1939). Such fitted curves may be regarded as describing the growth of the pigs more satisfactorily than the actual weights, because intermediate weighings can be utilized, changing rates of growth can be simply specified, and irregularities arising from the weighings of live pigs are smoothed out.

In this paper a second group of thirty-one pigs (five litters by three boars) unrelated to the first group of forty-four pigs, has also been considered.

METHOD OF ANALYSIS

The object has been to describe as briefly as possible the growth rate of the pigs from weaning onwards, but in such a way that changes in the rate were not merged into a single average. This was done by calculating orthogonal polynomials to the third degree according to the method of Aitken (1933). Logarithms of the live weights were used in the hope of minimizing the significance of the cubic term, and of avoiding undue emphasis on the variation in gains of live weight which may occur in the latter stages of fattening. To simplify the calculations, eleven weights for each pig in group I, and ten for each pig in the faster-growing group II were used. The last was obtained at the final regular fortnightly weighing before dispatch to the bacon factory. Working backwards from this, ten (or nine) more consecutive weights were taken, which meant that the average age of a pig at no. 1 weight was 10-12 weeks. An example of the calculation of the coefficients, and the test of their significance is given in Table I.

This particular example was not typical, but was chosen to illustrate a case in which the cubic term was large, and reference to the actual weights or to Fig. 1 (a) will indicate that this has arisen from a period following weaning in which apparently little growth took place. Fig. 1 (b) shows the actual and fitted growth curves for a pig more closely resembling the average animal. As shown by Aitken, the fitted values for each weighing can be readily calculated from the data in Table I. If the differences between these fitted values (Y) and the actual recorded values (y) are squared and summed, the value of $S(Y-y)^2$ obtained is the same as that remaining after the mean and the three coefficients have been

Table I. *Example of the fitting of a cubic curve and the testing for significance of the polynomial coefficients*

No.	x	Live weight lb.	Log	100 (log − 1·5)	S_1	S_2	S_3	S_4
1	− 5	54	1·73	23	581			
2	− 4	57	1·76	26	558	3632		
3	− 3	56	1·75	25	532	3074	11962	
4	− 2	80	1·90	40	507	2542	8888	25108
5	− 1	94	1·97	47	467	2035	6346	
6	0	116	2·06	56	420	1568	4311	
7	1	130	2·11	61	364	1148	2743	
8	2	151	2·18	68	303	784	1595	
9	3	170	2·23	73	235	481	811	
10	4	190	2·28	78	162	246	330	
11	5	217	2·34	84	84	84	84	84

$$(Sy^2 = 35589)$$

Terminal values and differences of Tchebychev polynomials $(n = 11)$

	a_0	a_1	a_2	a_3
581	1	− 5	15	− 30
3632		1	− 9	36
11962			2	− 20
25108				5
	11	110	858	4290

$$a_0 = \frac{581}{11} \qquad\qquad\qquad\qquad\qquad\qquad = 52\cdot81$$

$$a_1 = \frac{3632 - 5\,(581)}{110} = \frac{727}{110} \qquad\qquad\qquad = 6\cdot61$$

$$a_2 = \frac{2\,(11962) - 9\,(3632) + 15\,(581)}{858} = \frac{-49}{858} \qquad = -\ 0\cdot057$$

$$a_3 = \frac{5\,(25108) - 20\,(11962) + 36\,(3632) - 30\,(581)}{4290} = \frac{-378}{4290} = -\ 0\cdot088$$

Progressive elimination of regression variance

Degree k	a_k	Numerator	Product	$S(Y-y)^2$	D.F.	Mean square	Significance of reduction in variance
—	—	—	—	35589			
0	52·82	581	30688	4901	10	490·10	
1	6·61	727	4805	96	9	10·67	s.s.
2	− 0·057	− 49	2·8	93·2	8	11·65	N.s.
3	− 0·088	− 378	33·3	59·9	7	8·56	N.s.

Significance of cubic term: $F = 33\cdot3/8\cdot56 = 3\cdot89$, which is non-significant, the 5 % point being 5·59 for $n_1 = 1$ and $n_2 = 7$.

fitted as in the last part of Table I (in that example, 59·9). For the majority of the pigs the residual sum of squares lay between 10 and 30, which represents a mean square of 1·5–4·3, or a standard deviation of about 1·2–2·1 or 2–4 % per observation. Since they are based on logarithms, these values are not directly applicable to the actual weights.

For the purposes of this study, the formation of regression equations was not considered necessary. But to show the relation of the coefficients to the actual changes in growth rate, the basic form of the equation may
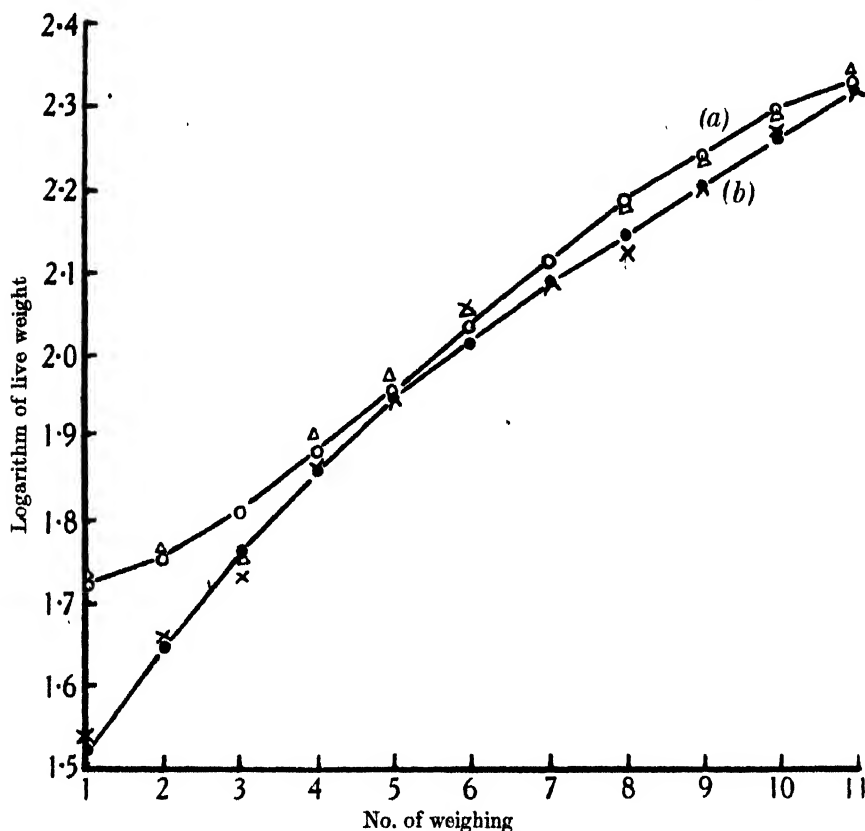
Fig. 1. Observed and fitted values of the logarithms of live weights of two pigs.

	(a)	(b)
a_0	+52·81	+47·82
a_1	+ 6·61	+ 7·62
a_2	− 0·057	− 0·350
a_3	− 0·088	+ 0·039
Observed values	△——△	×——×
Fitted values	○——○	●——●

be written down from the table of terminal values and differences as shown by Aitken, thus (for $n=11$):

$$Y = a_0 + a_1 (x-5) + a_2 \left[\frac{2x\,(x-1)}{1\,.\,2} - 9x + 15 \right] + a_3 \left[\frac{5x\,(x-1)\,(x-2)}{1\,.\,2\,.\,3} \ldots \right],$$

$$= a_0 + a_1 (x-5) + a_2 \left[(x-5)^2 - 10 \right] + a_3 \left[\ldots \right],$$

where Y is the estimated weight of a pig at a given time x. Since a constant number of weighings was used for the pigs of each group, the

terms following the a coefficients are the same in each group. The growth rates of the pigs may therefore be compared by means of the a coefficients alone. The mean of all the weighings is a_0. The average rate of growth, or the slope of the straight line fitted to the weights is represented by a_1 and the rates of change in growth rate by a_2. Since the weights are in the form of logarithms, a_2 represents changes in the relative rate of growth with increasing age.

Since some variation in the cold carcass weight was unavoidable, it has been thought advisable to introduce carcass weight (w) as an extra variable in order that the relation of carcass measurements to growth rate could be determined free of complications arising from that source. Moreover, the use of the a coefficients as the sole measures of growth is open to the objection that if weaning weight were correlated with them, any effects of pre-weaning growth would be inseparable from those associated with the coefficients representing post-weaning growth. Weaning weight (h) as a further independent variable was therefore included.

The carcass measurements (in mm.) selected for study were (a) loin length as from the first rib to the edge of the *symphysis pubis* bone; (b) leg length as from the latter point to the tip of the toe of the hindleg; (c) maximum thickness of fat at the shoulder; (d) thickness of fat at the level of the last rib: (e) thickness of fat over the middle of the rump muscle; and (f) breadth of eye muscle. With the exception of (f) the measurements were taken from both sides of the split carcasses and averaged for each pig; (f) was measured after curing from three rashers cut from one side at the level of the last rib.

<div align="center">RESULTS</div>

Table II shows the mean values for the fitted coefficients. In each group the hogs made faster growth than the gilts (a_1), but the rate slowed up more towards bacon weight (a_2), the downward curvature of the fitted line at its upper end being greater the larger the negative value of a_2.

Owing to the different numbers of weighings in the two groups, the average performance of each must be compared by means of the appropriate equations which are:

$$\text{Group I} \quad Y = 14 \cdot 58 + 9 \cdot 79x - 0 \cdot 306x^2,$$
$$\text{Group II} \quad Y = 11 \cdot 50 + 11 \cdot 70x - 0 \cdot 420x^2.$$

Table II. *Mean values of a coefficients, cold carcass and weaning weights (in lb.), and carcass measurements (in mm.) for groups I and II*

Group	a_0	a_1	a_2	a_3	Cold carcass weight (w)	Weaning weight (h)	No. of pigs
I. Hogs	51·6	6·97	−0·337	0·041	152	27·2	20
Gilts	53·8	6·53	−0·280	0·023	157	27·3	24
All pigs	52·8	6·73	−0·306	0·031	155	27·3	44
II. Hogs	50·7	4·19	−0·908	−0·013	158	29·7	15
Gilts	53·5	3·75	−0·785	−0·002	159	32·1	16
All pigs	52·2	3·96	−0·845	−0·007	159	31·0	31

	Length of		Thickness of fat at			Breadth of eye muscle
	Loin	Leg	Shoulder	Last rib	Mid-rump muscle	
I. Hogs	766	572	53·3	33·7	32·8	45·8
Gilts	788	573	49·1	31·6	31·2	47·7
All pigs	778	572	51·0	32·6	31·9	46·8
II. Hogs	783	585	53·6	31·9	33·7	47·1
Gilts	794	590	51·2	30·3	31·4	47·0
All pigs	789	587	52·4	31·1	32·5	47·1

The curve for group II was therefore steeper than that for group I (x), but showed greater curvature (x^2). This difference in curvature was probably due to the necessity of slowing up in the second group the growth of pigs waiting for fortnightly slaughterings. For present purposes, the difference in growth rate between the groups is advantageous since it increases the range of growth rates over which the following investigations apply. This range, in terms of the age at time of last weighing was 200–302 days for group I and 181–229 days for group II, and in terms of the weight put on during the 22 (or 20) weeks prior to slaughter was 132–188 lb. for group I, and 153–189 lb. for group II.

The fitting of a_0 and a_1, and of a_2 (with three exceptions) always significantly reduced the variance. Of the a_3 coefficients, thirty-six out of forty-four in group I and eleven out of thirty-one in group II were positive, and the rest negative. The fitting of eleven (ten positive) in group I, and of two (both negative) in group II, brought about a significant reduction in variance. Nevertheless, the a_3 coefficients derived from these logarithmic data were so small and variable in sign that they were thenceforth disregarded. Further, little interest attached to a_0, and attention was therefore fixed on a_1 and a_2.

Direct analyses of variance established sex differences in a_1, but not a_2. As reported previously (Donald, 1939), sex differences were found in the carcass qualities: loin length, thickness of fat at the shoulder and thick-

ness of fat at the level of the last rib, males being shorter and fatter than females. In what follows, therefore, variances and covariances have been calculated within sexes so that the regressions of carcass measurements on the a coefficients represent the weighted averages of the corresponding regressions for hogs and gilts. Litter differences were small and have been neglected. The analysis has thus been directed towards determining whether the observed variations in the carcass measurements within sexes were related to the variations in the corresponding coefficients a_1 and a_2, taking into account the cold carcass weight, and weaning weight.

The method of multiple regression given by Fisher (1936) and Snedecor (1938) was adopted. The calculation of c multipliers rendered the following calculations very simple and rapid. For each of the six carcass measurements the total correlations with the four independent variables were required from which to calculate the standard partial regression coefficients. As an example the procedure for loin length is given in Table III. For the other carcass measurements the same c multipliers were used, but each time with the appropriate set of four correlation coefficients. The standard partial regression coefficients are independent of units of measurement, and may be used to compare the

Table III. *Estimation of standard partial regression coefficients*
for loin length (b) in relation to a_1, a_2, w, and h

	b	a_1	a_2	w	h
Sum of squares	16,083	2605	7908	2130	1118
Sum of products:					
ba_1, ba_2, etc.		-1359	1848	2405	-24
a_1a_2, a_1w, etc.			-1811	-518	-67
a_2w, etc.				-334	-174
wh					-494
Correlation coefficients:					
r_{ba_1}, r_{ba_2}, etc.		-0.21	$+0.16$	$+0.41$	-0.01
$r_{a_1a_2}$, etc.			-0.40	-0.22	-0.04
r_{a_2w}, etc.				-0.08	-0.06
r_{wh}					-0.32

Solving:

$$c_1 - 0.40c_2 - 0.22c_3 - 0.04c_4 = 1 \quad 0 \quad 0 \quad 0$$
$$-0.40c_1 + \quad c_2 - 0.08c_3 - 0.06c_4 = 0 \quad 1 \quad 0 \quad 0$$
$$-0.22c_1 - 0.08c_2 + \quad c_3 - 0.32c_4 = 0 \quad 0 \quad 1 \quad 0$$
$$-0.04c_1 - 0.06c_2 - 0.32c_3 + \quad c_4 = 0 \quad 0 \quad 0 \quad 1$$

Solution	1	2	3	4
$c_1 =$	1·3300,	$+0.5780$,	$+0.4088$,	$+0.2186$;
$c_2 =$	0·5780,	$+1.2662$,	$+0.2899$,	$+0.1918$;
$c_3 =$	0·4088,	$+0.2899$,	$+1.2526$,	$+0.4348$;
$c_4 =$	0·2186,	$+0.1918$,	$+0.4348$,	$+1.1595$;

whence the standard partial regressions

$$\beta_{ba_1 \cdot a_2wh} = c_1 r_{ba_1} + c_2 r_{ba_2} + c_3 r_{bw} + c_4 r_{bh} = -0.0178 \text{ (solution 1)};$$
$$\beta_{ba_2 \cdot a_1wh} = c_1 r_{ba_1} + c_2 r_{ba_2} + c_3 r_{bw} + c_4 r_{bh} = +0.2042 \text{ (solution 2)};$$
$$\beta_{bw \cdot a_1a_2h} = c_1 r_{ba_1} + c_2 r_{ba_2} + c_3 r_{bw} + c_4 r_{bh} = +0.4739 \text{ (solution 3)};$$
$$\beta_{bh \cdot a_1a_2w} = c_1 r_{ba_1} + c_2 r_{ba_2} + c_3 r_{bw} + c_4 r_{bh} = +0.1576 \text{ (solution 4)}.$$

relative importance of a_1, a_2, w (cold carcass weight), and h (weaning weight), as factors in the variation of the carcasses. Thus Table III shows that the partial regression of loin length on carcass weight ($\beta_{bw} = +0\cdot4739$) was more than twice as great as that of loin length on either a_1, a_2 or h.

The partial regressions now available were used to estimate the total correlation (R) from the formula

$$R^2 = r_{ba_1}\cdot\beta_{ba_1.a_2wh} + r_{ba_2}\cdot\beta_{ba_2.a_1wh} + r_{bw}\cdot\beta_{bw.a_1a_2h} + r_{bh}\cdot\beta_{bh.a_1a_2w}.$$

R^2 sums up in a convenient way the proportion of the total variance which is accounted for by the dependence of the carcass measurements on the four variables a_1, a_2, w and h. What is left $(1 - R^2)$ of the total variance represents variations in carcass quality still uncontrolled. The significance of R and thus of the reduction in variance due to correction for multiple regression may be read off the appropriate tables (Snedecor, 1938).

The standard partial regression coefficients were also tested for significance separately. For example, the coefficient $\beta_{bw.a_1a_2h} = +0\cdot4739$ had a variance of $\dfrac{1-R^2}{\text{D.F.}}\cdot c_{33}$, the square root of which was $\pm0\cdot1591$. The coefficient was therefore $2\cdot98$ times its standard error, and significant at the 1% point (D.F. $=38$).

A summary of the calculations for all the carcass measurements is given in Table IV.

Table IV. *Standard partial regression coefficients*
($n = 44$ in group I and 31 in group II)

		Length		Thickness of fat			Breadth of eye muscle
	Group	Loin	Leg	Shoulder	Last rib	Mid-rump muscle	of eye muscle
a_1	I	$-0\cdot02$	$-0\cdot30$†	$+0\cdot06$	$+0\cdot24$	$+0\cdot06$	$-0\cdot01$
	II	$+0\cdot25$	$+0\cdot02$	$+0\cdot03$	$+0\cdot03$	$+0\cdot43$†	$-0\cdot14$
a_2	I	$+0\cdot20$	$+0\cdot02$	$+0\cdot07$	$+0\cdot20$	$-0\cdot07$	$-0\cdot21$
	II	$-0\cdot27$	$+0\cdot29$	$+0\cdot01$	$+0\cdot09$	$+0\cdot09$	$-0\cdot31$
w	I	$+0\cdot47$*	$+0\cdot52$*	$+0\cdot18$	$+0\cdot11$	$+0\cdot13$	$+0\cdot08$
	II	$+0\cdot26$	$+0\cdot55$*	$+0\cdot38$†	$+0\cdot46$*	$+0\cdot29$	$+0\cdot03$
h	I	$+0\cdot16$	$+0\cdot40$*	$-0\cdot27$	$-0\cdot06$	$-0\cdot23$	$+0\cdot19$
	II	$+0\cdot25$	$+0\cdot42$*	$-0\cdot24$	$-0\cdot75$*	$-0\cdot28$	$+0\cdot12$
R^2	I	$+0\cdot23$†	$+0\cdot47$*	$+0\cdot14$	$+0\cdot07$	$+0\cdot10$	$+0\cdot08$
	II	$+0\cdot38$†	$+0\cdot53$*	$+0\cdot17$	$+0\cdot67$*	$+0\cdot35$†	$+0\cdot13$

a_1, a_2, fitted coefficients;   *, significant at 1% point;
w,   cold carcass weight;   †, significant at 5% point.
h,   weaning weight.

It is to be borne in mind that the regression coefficients in Table IV refer not to the original units of measurement but to units equal to the

standard deviation of the variables. Thus the coefficient $+0.47$ for loin length and carcass weight in group I means that when adjustment is made for a_1, a_2 and h, an increase in carcass weight equal to the standard deviation in carcass weight was associated with an increase in loin length of 0.47 of the standard deviation of loin length. Another point to remember is that values of a_2 are negative and therefore the signs of the regression coefficients are affected.

Genetically, the pigs of group I were probably more alike than those of group II. The former were all by the same boar, while the latter were out of sows unrelated to the first lot and by three other boars. Further, group II pigs were 11 mm. longer in the loin than group I pigs, 15 mm. longer in the hindleg, but just as fat along the back. These details of breeding and conformation are of interest in considering the response of each group to the changes in growth rate.

(1) *Loin length.* The values of R^2 show that correction for the four independent variables has resulted in a reduction of "error" variance by one-quarter or more. The sources of the reduction are, however, not equally important in the two groups and consequently it is not possible to predict with assurance what would happen in other samples of pigs. It may be assumed that carcass weight has a real effect on loin length, and probably also weaning weight, because the two coefficients, although not significant, agree reasonably well with each other and in direction with the corresponding coefficients for leg length. The influence of a_1 and a_2 was non-significant in both groups, and therefore small or negligible. The difference between the coefficients for a_2 is rather wide and suggestive of an unlike response by the two groups such that with an increasing rate of decline in relative growth rate, loins became longer in group II than in group I.

Within a limited range of growth rates, loin length seems to depend mainly on body weight and but little on the rate at which that weight was attained. The present figures support those of Mansfield *et al.* (1937), who found that the average loin length of fifty pigs on an unrestricted diet was the same as that of fifty restricted pigs reaching bacon weight 35 days later.

(2) *Leg length.* The evidence here is unmistakeable that weaning weight and carcass weight have modified leg length. Heavy weaners and heavy baconers have had longer legs than light weaners and baconers, and allowance for this fact has resulted in decreasing uncontrolled variation by one-third to one-half. But here too the effects of growth rate are unlike in the two groups.

In group I, short legs have been associated with high values of a_1 (that is, steep growth curves), whereas in group II they have been associated with high negative values of a_2 (that is, curves showing rapid decline in relative growth rate towards the end). McMeekan & Hammond (1939) observed that their fast-growing pigs had a low proportion of head and legs compared with slow-growing pigs, and it might have been expected therefore that the faster-growing group II pigs would have had shorter legs than the slower-growing group I pigs. Reference to Table II will show that the reverse was the case, group II pigs being distinctly leggier in type. Although the data require cautious interpretation, it is interesting to speculate whether the failure of the long-legged group II pigs to conform with those of group I and of McMeekan & Hammond is due to a retention to a greater age of the tendency in both groups for fast growth up to weaning to lead to greater leg length. Such differences as these might be expected in pigs since they are born with short legs that have to undergo a period of rapid growth during which they may readily respond to both genetic and environmental influences. With grazing animals, like sheep and cattle, the new-born have relatively long legs, the growth of which, after birth, is slower and probably less susceptible to modification.

(3) *Thickness of fat at the shoulder.* For this character, the regression coefficients show much uniformity. The rate of growth has been unimportant, but as might have been expected, carcass weight has probably affected the thickness of fat. The coefficients for weaning weight fall short of significance, but since they agree well, it seems likely that heavy weaners developed less shoulder fat. This would be in keeping with the greater growth in length of bone observed in the same pigs, provided more bone meant less fat at constant weight. The reduction in variance achieved has been comparatively small.

(4) *Thickness of fat at the level of the last rib.* There are notable differences here in the behaviour of the two groups of pigs. Group I coefficients for a_1 and a_2, though not significant, agree that there was a tendency for fast growth and thick fat to go together, but in group II the tendency was very slight. Further, both carcass and weaning weight have affected group II very noticeably, but group I hardly at all. The result is that control of variation is very substantial in group II and negligible in group I.

(5) *Thickness of fat above the middle of the rump muscle.* At this point group II pigs have become more susceptible to differences in growth rate (a_1) and group I pigs less so. This, in conjunction with (4) above, suggests

that the two groups were of different types from the point of view of development of back fat. The influence of weaning weight has, however, been similar in both groups as it was for shoulder fat, the heavy weaners developing less fat than the light.

(6) *Breadth of eye muscle.* This character appears to have been resistant to modification by any of the variables studied, for very little control of variation has been secured. The most that can be said is that a slowing up of growth in the late stages of fattening may have been responsible for the observed thickening of the eye muscle in pigs with large negative values of a_2, but the effects have not been great enough to yield statistical significance. Using other variables, Crampton (1938) found variation in this character equally difficult to account for.

(7) R^2. The values of R^2 give the portion of the total variance which arises from the regression of the dependent carcass measurements on the independent variables, a_1, a_2, w and h. Table IV shows that adjustment for these regressions has resulted in a considerable reduction in the observed variance of leg and loin length, and sometimes in the variance of other carcass measurements. In so far as certain numerically large, but non-significant, values of the correlation between pairs of variables are fortuitous, it cannot be assumed that in other samples of pigs equal reductions in variance can be achieved by the same corrections. The present results do show, however, that under some circumstances the corrections may be large enough to influence appreciably the magnitude of the carcass differences between groups of tested pigs which can be detected by statistical methods. They show also that some parts of the carcass are more susceptible to modification than others, but the order of susceptibility is not necessarily the same in distinct strains of pigs.

Loin length and thickness of back fat

Although the main purpose of this study is to circumscribe variation, it is of interest to consider the results in the light of published accounts of carcass quality variation. Judged merely by their statistical results, there is a disconcerting lack of agreement among them. As an example, the relation between loin length and thickness of back fat may be cited. Lush (1936) compared the results of Jespersen and Madsen with his own from Danish pigs, and points out that their correlations of -0.197 (based on 3577 hogs) and -0.145 (based on 3382 gilts) are lower than his estimate of -0.39 (based on the means of 1285 tested litter samples). The reason for the differences between such large samples is not clear, but it may be connected with genetical changes induced in the breeding stock by

selection. Again, in Canada the same correlation calculated by Sinclair & Murray (1935) and by Stothart (1938) for shoulder fat was small and non-significant. These authors emphasize the genetic variability of their pigs, which may have been responsible for obscuring any relationship of loin length and thickness of back fat.

The results obtained from the present data show an interesting difference in Table V, which gives the standard partial regression of back fat at three levels on loin length.

Table V. *Standard partial regression of back fat on loin length.* (a) a_1, a_2 *and carcass weight held constant;* (b) *carcass weight and weaning weight held constant*

		Shoulder	Last rib	Mid-rump muscle
(a)	Group I	- 0·58	− 0·49	− 0·37
	Group II	− 0·16	− 0·10	− 0·19
(b)	Group I	− 0·50	− 0·45	− 0·35
	Group II	− 0·06	+ 0·09	+ 0·06

Group I exhibits a much closer dependence of back-fat thickness on loin length than does group II. This contrast between the groups cannot be attributed to the shape of the last 20–22 weeks of the growth curve, nor to differences in weaning weight or carcass weight. But genetic differences in conformation might account for the discrepancy. At a constant weight, long and short carcasses cannot have the same conformation, but the difference may not always be expressed in the same way. Thus in some strains extra length brings thinner back fat; in others it may bring thin bellies or narrow sides.

DISCUSSION

The value of the statistical technique of fitting polynomial coefficients to growth records can hardly be judged fairly until more is known of the physiological nature of growth. There are various ways of describing a growth curve and their usefulness depends on their suitability for the purpose in hand. The simple method of calculating differences between initial and final weight is open to objections, including its failure to take previous history into account. Similarly the more sophisticated fitting of curves of any kind to serial data may entail neglect of some essential fact in spite of giving a very accurate description of the observed changes. The use of total live weight as a measure of growth is probably unsound in quantitative studies of body tissues, since it is a composite of the changing weights of all tissues and organs, each of which has its own rate

of development. Nevertheless, an animal exists as a unit, so that there must be harmony and integration of its component parts and its internal functioning. The fact that a pig retains to a considerable degree its power to express its own type and develop true to an inborn pattern under diverse conditions, is the external expression of this internal regulation.

To appreciate the remarkable resilience of animals to changing conditions, one need only think of the experiments of McCay *et al.* (1935) and Jackson (1936, 1937), who found that rats subjected to long periods of arrested growth by under-feeding while still young, later attained almost normal body size and proportions when adequately fed. In experiments of a somewhat similar nature with pigs, however, McMeekan & Hammond (1939) observed that extreme differences in plane of nutrition did affect the proportions of bone, muscle and fat in the resulting carcasses. Compared with the treatments which were necessary to produce them, the differences obtained may not appear very great, but from the point of view of carcass quality, they were most important. The question which this study set out to answer was whether or not the growth rate differences and changes in groups of pigs raised for bacon in the customary way had affected carcass quality. As far as these pigs are concerned, the answer is that growth rate did affect carcass quality, but that the extent of its effects varied with the part of the carcass, with the time at which the growth rate was measured, and with the genetical constitution of the pigs. Thus, good growth up to weaning has favoured bone and muscle growth at the expense of fat in the carcass, and fast growth after weaning, though of no importance in several measurements, has influenced others in the direction of more fat and less muscle.

So far as they go, therefore, these results agree with the conclusion of McMeekan & Hammond, that maximum leanness in pigs destined for bacon is obtained by securing rapid growth while the pigs are young, and by limiting the rate of growth (and therefore the rate of fat deposition) as they approach bacon weight.

As a factor in the control of variation in carcass quality, however, growth rate would appear to become rapidly less important than other factors (such as hereditary differences in type and conformation) as the extremes of growth rate approach each other. This applies, of course, to conditions of rearing in which both hereditary and environmental influences on the growth and development are at work. When hereditary variation is limited and environmental variation emphasized, as in the Cambridge experiments, the effects of the latter may be expected to be more clearly defined.

Reference to the foregoing tables will show that differences between individual measurements provided the. bulk of the variation even when growth rate and carcass weight were held constant. The position would appear to be, therefore, that while hereditary type is likely to be the principal factor in carcass quality, animals deviating from the ideal may be modified towards it by adjusting the rearing conditions. Experience with the relationship of loin length and back fat, however, points to the need for caution in applying the results with any given strain of pig to pigs in general, for it seems possible that the response to raising or lowering the plane of nutrition may not be the same in pigs which are naturally unlike in conformation.

SUMMARY

1. An examination of carcass reports from two groups of bacon pigs (comprising eleven litters and seventy-five pigs) was made to determine whether the variation in growth rate of normally reared pigs was associated with differences in carcass measurements. The method adopted was to fit orthogonal polynomials to the third degree to the last 10–11 fortnightly weighings converted to logarithms.

2. The residual standard deviation after fitting was about 2–4 %. For present purposes, the fitting of second degree parabolae appeared adequate.

3. By means of standard partial regression coefficients, the dependence of each of six carcass measurements on growth rate (a_1), rate of change of growth rate (a_2), carcass weight, and weaning weight, was determined. Both loin and leg length tended to increase as weaning and carcass weights increased, but the response to variations in a_1 and a_2 was neither marked nor consistent in the two groups, possibly owing to a difference in type. Thickness of shoulder fat was negatively correlated with weaning weight, but unaffected by variation in a_1 or a_2. Thickness of fat at the level of the last rib was very responsive to differences in weaning weight in one group, but not in the other, while over the middle of the rump muscle the degree of dependence on weaning weight was about the same in both groups. A tendency was observed for fast growth after weaning and thick back fat to be associated, but this was shown by one group above the last rib, and in the other over the rump muscle. Breadth of eye muscle appeared to be largely independent of all the variables, although in both groups a tendency falling short of significance was found for the muscle to become thicker as the rate of decline of relative growth rate towards bacon weight increased.

4. Statistical control of variation in carcass measurements by adjustment for regression on the four independent variables was greatest for loin and leg length (amounting to a reduction in variance of about one-quarter to one-half) and least for shoulder fat and breadth of eye muscle for which it did not reach the level of significance. The adjustments applied to thickness of fat at last rib and mid-rump muscle were very small and non-significant in one group, and substantial and significant in the other, reaching 67 % for thickness over the last rib.

5. The dependence of thickness of back fat on loin length was strong in one group and weak in the other. The difference is probably genetic in origin, and suggests an explanation for the discrepancies among published results.

6. Since the influence of growth rate on carcass measurements appears to have been expressed in a variable way according to type of pig concerned, it may be unwise to make detailed predictions of the relation between growth rate and carcass quality.

The difficulty of establishing effects of growth rate after weaning on carcass measurements suggests that within a limited range of variation in growth rate, these effects tend to be small, inconsistent, and relatively less important than individual type.

REFERENCES

AITKEN, A. C. (1933). *Proc. Roy. Soc. Edinb.* **53**, 54-78.

CRAMPTON, E. W. (1938). *Sci. Agric.* **19**, 155-61.

DONALD, H. P. (1939). *Proc. VI Internat. Congr. Animal Breeding, Zurich.*

FISHER, R. A. (1936). *Statistical Methods for Research Workers.* Edinburgh: Oliver and Boyd.

JACKSON, C. M. (1936). *Amer. J. Anat.* **58**, 179-93.

—— (1937). *Amer. J. Anat.* **68**, 371-81.

LUSH, J. L. (1936). *Res. Bull. Iowa agric. Exp. Sta.* no. 204.

MANSFIELD, W. S., TREHANE, W. R. & PEACOCK, R. B. (1937). *J. Roy. agric. Soc.* **98**, 172-85.

McCAY, C. M., CROWELL, M. F. & MAYNARD, L. A. (1935). *J. Nutrit.* **10**, 63-79.

McMEEKAN, C. P. & HAMMOND, J. (1939). *J. Minist. Agric.* **46**, 238-43.

Sinclair, R. D. & Murray, J. A. (1935). *Sci. Agric.* **16**, 169–174.

Smith, A. D. B. & Donald, H. P. (1939). *J. agric. Sci.* **29**, 274–94.

Snedecor, G. W. (1938). *Statistical Methods.* Iowa: Collegiate Press, Ames.

Stothart, J. G. (1938). *Sci. Agric.* **19**, 162–72.

Wishart, J. (1938). *Biometrika,* **30**, 16–28.

—— (1939). *J. Roy. Stat. Soc.* Suppl. **6**, 1–22.

THE "RESTRICTED" FEEDING OF BACON PIGS

A CO-ORDINATED EXPERIMENT AT CENTRES IN GREAT BRITAIN AND IRELAND

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INTRODUCTION

ONE of the most controversial questions that has arisen in connexion with the fattening of bacon pigs concerns the level of feeding, or "plane of nutrition", that should be followed.

Whilst it has long been held that the quickest gains are the most economical and that feeding to the maximum allowed by appetite is the best rule to follow, this view has been contested in recent years. There is a good deal of evidence to suggest that some form of restriction of the meal ration not only ensures more economical utilization of the food supplied but also produces carcasses of better quality. This limitation of the amount of meal consumed may be brought about either by a simple quantitative restriction of the ration so that the appetite of the pig is not fully satisfied or, alternatively, the bulkiness of the feed may be so increased that, whilst appetite may still be satisfied, the actual production value of the ration eaten is considerably reduced. It is with the former type of "restricted" feeding that this paper is concerned.

"Restriction", however, is a wide term and has been interpreted in a variety of ways; almost every experiment which has been carried out has approached the question in a different manner and any uniformity of design is lacking.

The earlier work on this subject has been done in America and typical rations employing high proportions of maize with supplements of "tankage" have been used. Ferrin & McCarty (1928) compared pigs full-fed from a self-feeder with those receiving only half this amount of meal up to 150 lb. and then full-fed. They obtained not only better rates of gain with the former but also more economical food conversion. Ellis & Zeller (1931), on the other hand, report five experiments in which full-fed pigs were compared with others on rations restricted to 75, 60 or 50% of the quantity given to the former. The basal ration consisted, in three cases, of shelled pea-nuts, and of corn in the other two, with

supplements of "tankage", linseed meal, lucerne meal and minerals. Restriction was associated with more economical gains and a reduction in total body fat, but the softness of the carcass was increased. Similar results were obtained in later experiments (Ellis & Zeller, 1934) in which self-fed pigs were compared with those restricted to 70, 60 or 50% of the allowance of the former. St Pierre *et al.* (1934) also found that pigs receiving 75% of the amount eaten by those which were given all they could readily clear up twice daily made more economical gains, but that restriction to 50% was unsatisfactory. Pigs on both the reduced levels of feeding tended to have softer carcasses, with lower dressing percentages. Crampton (1935) found no advantage from restriction to 50% of full-feeding level, in either economy of food conversion or in grading results, and Freeman (1935), limiting the ration of 60 lb. pigs to the equivalent of 2 and 3% of the live weight, obtained poor food-conversion figures compared with those for self-fed pigs. The effect on carcass quality was not determined.

In Great Britain, Mansfield & Trehane (1935) fed matched pairs of pigs individually and compared full feeding with restriction to three-quarters of this amount from 65 to 100 lb. and to two-thirds from 100 to 200 lb. It may be remarked, in parenthesis, that the average ration per head for the full-fed pigs amounted to the high figure of 5·57 lb. a day and, for the restricted ones, 3·92 lb. Economy of food conversion and grading results were both improved by the lower level of feeding. Similar results were obtained in a second experiment (Mansfield & Trehane, 1937). In a third comparison, carried out by the same experimenters (1937), the ration of the restricted pigs was no longer made to depend on the amount of food consumed by the full-fed ones but increased according to a scale from 3 lb. a head daily at 60–69 lb. to 5⅓ lb. at 190 lb. Results were inconclusive and fourteen of the restricted pigs showed soft fat due, it was considered, to the combination of slow fattening and very cold weather conditions. Improvements in economy of food conversion and grading by feeding 87½ or 75% of the amount consumed by full-fed pigs have also been reported from Cheshire (1938). In experiments reported from Rothamsted (1935), however, restriction of feeding failed to produce significant effects on efficiency of food conversion or carcass grading. In the first of these, three levels of restriction were compared with *ad lib.* feeding, pigs of an initial age of about 18 weeks being used. For the first 5 weeks the higher rates of feeding gave more efficient food conversion, but this difference did not persist throughout the remaining 10 weeks of the trial. In the second experiment, pigs were

limited to 90% of the full-feeding allowance after a live weight of 125 lb. and taken up to an average final weight of 180 lb.

Under group-feeding conditions, Crowther (1937) describes two experiments in which restriction to 90, 85 and 80% of the quantity allowed under full-feeding was imposed at 65, 85 or 100 lb. live weight. Whilst no difference between the effects of the various degrees of restriction or the times at which they were imposed was detected, restriction, on the whole, resulted in better food utilization and, in the first experiment only, thinner back-fat. In a third experiment pigs were full-fed until eating 2½ or 4½ lb. per day (Crowther & Heap, 1938); thereafter the ration increased weekly by ¼ lb. per pig to a maximum of 5½ lb. There was no appreciable difference in results between these pigs and those full-fed to 6½ lb. At the Midland Agricultural College (1938) pigs fed up to a maximum of 5½ lb. daily have been compared with those fed up to 7 lb. No differences in economy of food conversion were evident, but grading results were said to be in favour of the high plane, though no details are quoted.

At Reading, Huthnance & Campion (1936) compared pigs fed according to the recommended standards of Wood (1927) with others restricted to 10% below this level. The latter showed significantly better efficiency of food conversion, but grading differences were negligible. In a second experiment pigs were fed at the recommended level until eating 4½ lb. of food per day, at which figure the consumption was maintained. This degree of restriction was unfavourable, the food consumption being 0·34 lb. more per lb. live-weight gain than that of pigs on the higher scale.

In other experiments in this country the full-fed pigs have obtained their meal from self-feeders. In Scotland, Blissett (1935) and Biggar (1937) found less economical use was made of the meal and worse grading achieved by pigs allowed their food *ad lib.* from self-feeders than by those fed according to the scale of rationing recommended by the Scottish Agricultural Colleges. On this scale, pigs of about 40 lb. get 2 lb. of meal daily, increasing weekly by ¼ lb. per pig per day up to a maximum of 6 lb. Differences in results between two types of self-feeders were also obtained. In Northern Ireland, Baskett *et al.* (1937) compared groups of pigs fed as much wet meal as they could readily clear up in 10–15 min. three times a day with others receiving dry meal from self-feeders, to the advantage of the former in economy of food conversion and grading results. Under New Zealand conditions, Ballinger (1938) reports improved grading results from restricting the allowance of skim milk to fattening pigs, compared with the general practice of feeding this *ad lib.*,

but the effect upon the efficiency of utilization of the ration is not mentioned.

The results which are quoted above present a great diversity of experience. Bearing in mind the great differences which undoubtedly exist between different breeds, and between strains or types within breeds, in regard to such points as early maturity, thriftiness and general carcass characteristics (Hammond & Murray, 1937; Crampton, 1939), this is perhaps not surprising. Furthermore, when only small numbers of pigs are involved the experimental error is inevitably large, and in most of the experiments described the design was not such as to allow any valid estimate of this to be made, in consequence of which many of the results obtained can be accepted, at the best, only with caution. There was obviously a need for a properly co-ordinated enquiry into the merits of a practical degree of restriction, and one in which, by utilizing a suitable experimental design, the results would be capable of statistical analysis.

The co-ordinated experiment

The experiments to be described were carried out during 1938 and 1939 at fourteen centres in Great Britain, following a common experimental design drawn up by the Ministry of Agriculture's Pig Experiments Co-ordinating Committee. Details of the centres which co-operated are given in Table I. Of the fourteen centres which took part thirteen carried out group feeding; at the remaining one individual feeding was possible. Some centres were able to repeat the experiment so that altogether twenty-two trials were carried out, twenty-one of these being on group-feeding lines, and nearly 400 pigs were included. In Table I the centres have been divided into two groups according as to whether the experiment was commenced in summer or in autumn; it was conceivable that the response to the treatments might vary with seasonal conditions. This grouping has been maintained throughout this report. The pigs utilized in the experiment were, with two exceptions, home-bred and drawn from the herds run at the various centres. As Table I shows, they were all either Large Whites or Large White crosses.

The experiment was designed to compare three scales of feeding after the pigs had reached 100 lb. live weight. A "preliminary period" commenced when pigs were 70 lb. in weight; up to this stage they received the treatment normally practised at the respective centres. From 70 lb. they were fed the mixture "A" given in Table II and, up to 100 lb.

Table I. *Details of centres taking part in experiment*

Experimental centre	Breed of pig	Origin	No. of pigs per pen	No. of pigs put on experiment	No. of pigs despatched to factory	Date of commencement of experiment	Last delivery to factory
I. Group-fed pigs:							
A. Centres starting in summer:							
1. Agricultural Research Inst. of N. Ireland	Large White	Home bred	9	27	27	July 1938	14. xi. 38
2. Dauntsey's School, Wilts	L. White × Wessex	"	8	24	20	August 1938	5. x. 38
3. Lancs County Inst. of Agriculture	Large White	"	8	24	23	"	5. xii. 38
4. Monmouth C.C. Inst. of Agriculture	Large White	"	6	18	17	July 1938	3. xi. 38
5. Herts Inst. of Agriculture	Large White / L. White × Wessex	"	5	10	10	"	9. xi. 38
6. Kirton Agricultural Inst.	L. White × Essex / L. White × L. Black / Large White	"	6	18	15	June 1938	27. ix. 38
7. Harper Adams Agricultural College	Large White	"	5	30	30	"	6. x. 38
8. Midland Agricultural College	L. White × Tamworth	"	6	18	18	May 1938	22. ix. 38
9. Cumberland and Westmorland Farm Sch., Newton Rigg	Large White	"	6	17	16		12. ix. 38
10. Durham School of Agriculture	Large White	Bought	6	18	17	July 1938	12. x. 38
B. Centres starting in autumn:							
11. Dauntsey's School, Wilts	Large White	Home bred	9	27	27	November 1938	22. ii. 39
12. Hampshire County Farm Inst.	"	"	7	21	20	December 1938	22. iii. 39
13. Askham Bryan Farm, Yorkshire	"	"	5	15	15	October 1938	5. i. 39
14. Somerset Farm Inst.	L. White × Wessex	Bought	6	18	17	September 1938	29. xi. 38
15. Harper Adams Agricultural College	Large White	Home bred	5	90	86	December 1938	20. iv. 39
II. Individual feeding:							
16. Cheshire School of Agriculture	Large White	Home bred	—	18	18	August to September 1938	8. xii. 38
			Total	393	376		

live weight, all pigs were fed according to the same scale; by the time they had reached the latter weight they were getting 4 lb. of meal per head daily. Thereafter, rationing according to three scales of feeding was followed; these were:

I. "High" scale; pigs received daily 4 lb. meal plus 1 lb. for every 20 lb. increase in weight above 100 lb.

II. "Medium" scale; pigs received 4 lb. meal plus $\frac{2}{3}$ lb. for every 20 lb. increase in weight above 100 lb.

III. "Low" scale; pigs received 4 lb. meal plus $\frac{1}{3}$ lb. for every 20 lb. increase in weight above 100 lb.

In each case there was no increase in the amount of food fed after a live weight of 170 lb. was reached. At this stage pigs on the three feeding scales were receiving respectively 7 lb. 8 oz., 6 lb. 5 oz., and 5 lb. 3 oz. of meal per head daily. The degree of restriction brought about by the above scales of rationing may be expressed in another way. It will be found that at a live weight of 115 lb., the amount of food received by pigs on the lowest scale is 90% of the allowance of those on the highest. At 135 lb. it is 80%, at 150 lb. 75%, and at 165 lb. has dropped to only 70%.

At 140 lb. live weight the composition of the ration fed was changed to that of mixture "B" in Table II, and this was fed until the end of the experiment. Pigs were slaughtered as near to 200 lb. as was conveniently possible; in order to make up reasonably sized groups for consignment to the factory there was naturally some variation in the weight at which pigs were despatched.

Table II. *Composition of ration (parts by weight)*

		Weatings	Barley meal	Flaked maize	White fish meal	Extr. soya bean meal	Minerals	Lucerne meal
A.	From 70–140 lb. live wt.	30	38	20	7	3.	2	2
B.	From 140 lb. to slaughter	30	43	20	—	5	2	2

In the group-feeding experiments one pen was allotted to each treatment. The number of pigs in a pen varied from five to nine as shown in Table I, and was such as to make the best use of the accommodation. As far as possible each of the pigs in a pen corresponded in sex, litter, origin and initial weight to a pig in each of the other pens, so that these were strictly comparable. The actual treatment to which the

members of each set of matched pigs were allocated was determined by random selection.

In following the scales of rationing, the amount of food fed to a pen was the sum total of the allowance each pig was entitled to receive, on the basis of its live weight, according to the scales given above. The change from mixture "A" to mixture "B" was made when the average weight of the pigs in the pen was 140 lb. Pigs were weighed individually once a week, and adjustment of the daily allowance of meal was made at the first feed on the day following weighing. Thus the daily meal allowance for any pen remained constant for each period of a week. Pigs were fed twice daily; water was mixed with the meal at the time of feeding.

Three pens of pigs corresponding to the three treatments were run at each centre except at the Hertfordshire Institute and at Harper Adams College. At the former only two pens were used, being allotted to treatments II and III. At Harper Adams, the experiment was run in duplicate in the summer with six pens and in the autumn was replicated six times, using, in all, eighteen pens, each accommodating five pigs.

In the individual-feeding experiment at the Cheshire centre, each pig, of course, received the exact amount of food determined by the feeding scales, and the mixture was changed at the appropriate time for each. Apart from feeding times, however, the pigs lived together four or five in a pen.

CARCASS RECORDS

As pigs reached the slaughter weight of 200 lb. they were dispatched in convenient numbers to the factories; as far as possible the latter were those normally utilized by the centres concerned. Transport was by road or rail and conditions were by no means uniform. Carcass measurements would undoubtedly be influenced by these differences (Bacon Development Board, 1938), though to what extent it cannot be said. Through the co-operation of the Food Investigation Board of the Department of Scientific and Industrial Research, the Bacon Development Board and the factories, the following carcass records were obtained of all the pigs slaughtered:[1]

(1) *The hot carcass weight*, i.e. the weight of the dressed carcass including the skin, head with tongue, kidneys, tender-loins ("fillets"), flare fat, tail, backbone and feet, but after removal of guts, pluck, etc.

(2) *The length of the body cavity* measured between the lower edge of

[1] Except those from the first experiment at Dauntsey's School, where the identity of some pigs was lost.

the aitch bone (pubis symphysis) and the junction of the first rib with the backbone.

(3) *The depth of the carcass* taken at the deepest point between the foreleg and the last rib.

. (4) *The length of the hindleg* measured from the lower edge of the aitch bone to the tip of the toe.

(5) *The length and weight of the foretrotter.*

(6) *The thickness of the back-fat.* This was measured at five places: (i) At the thickest point over the shoulder (A). (ii) At the thinnest point over the middle of the back (B). (iii) At three places over the rump muscle (C_3, C_2, C_1).

(7) *The thickness of the flank, or belly,* at a point opposite the junction of the fourth and fifth vertebrae below (i.e. nearer the head than) the bend of the backbone.

(8) *The weight of the flares,* i.e. the fat of the body cavity, surrounding the kidneys. This weight, considered in relation to the total carcass weight, gives some indication of the degree of fatness of the pig but cannot be regarded as a very accurate measurement.

(9) *The weight of the fillets,* trimmed so that only the psoas major muscle is weighed. This weight considered in relation to the total weight gives an indication of the degree of leanness of the carcass.

(10) *The weight of the kidneys.* In general this increases in proportion to the work thrown upon them.

All measurements were taken on the right and left sides and averaged. The length of the body cavity and of the hindleg were taken as soon as possible after the carcass was weighed and before the head had been removed or split away from either side of the carcass. The back-fat and flank were measured 4–6 hr. after slaughter. In addition to the records, a sample of the back-fat from near the tail was taken from each pig and removed to the Low Temperature Research Station, Cambridge, where the refractive index of the fat, which is correlated with iodine number and degree of softness (Callow, 1935), was determined.

Experimental results

Method of analysis

Before presenting the results of the experiment a brief explanation of the method of analysis adopted is desirable in order that the basis on which conclusions are drawn may be understood. This has been dealt with more fully elsewhere (Shorrock, 1940). At each centre carrying

out group feeding the design of the experiment was comparable, to a certain extent, with that of a simple randomized block lay-out in crop experimentation. The number of "blocks" at each centre was equal to the number of pigs in a pen, for each one of these corresponded, as has been said, to a pig in each of the other two pens on the experiment. The rate of live-weight gain per day can be obtained for each individual pig, and each pig also has a complete set of carcass records. In regard to food consumption, however, only a figure for each pen as a whole is obtainable in group feeding.

Thus, whilst tests of significance within each centre can be made on data concerning rate of live-weight gain, and on carcass records (though their validity is open to some doubt), this is not possible for food consumption figures, unless, as at Harper Adams College, the pens are replicated. It is in the combined data of all the experiments, however, that we are most interested. The method by which these may be analysed is outlined by Snedecor (1938) and by Yates & Cochran (1938), who discuss also the various complications which may arise. As it is desired to draw conclusions which may be applicable to the pig population of which those contributed to the experiment may be regarded as a sample, the appropriate estimate of "error" with which the average treatment effect should be compared will be that obtained from the differential response of centres to the same treatment—in other words, from the "interaction" of "treatments" with "centres". In the tables which are given later in this report it is this estimate of error which has been included.

On the other hand, the estimates of "error", or uncontrolled variation, obtained from the analysis of the data at each centre separately may be pooled and will be associated with the sum of the degrees of freedom for error contributed by each centre. Against this "pooled" estimate the significance of the differential response of centres to the same treatments may be tested, as also may the average treatment effect. In this case, however, we shall be concerned simply with the response of *these* pigs at *these* particular centres, and shall not be regarding them as a sample of the pig population as a whole.

It is not necessary to have the same number of "blocks" at each centre, and in the combined results which are given later the full number has been utilized; no information, therefore, has been sacrificed. In some cases, where the record of an animal is for some reason missing, its value has been calculated by the method described by Yates (1933), due allowance for this being made, of course, in the estimation of the standard error.

A. *Pre-slaughter results.*

(1) *General progress of pigs on the experiment.* The progress of the pigs on the experiment was on the whole very satisfactory, and at most centres little difference was to be noticed between the different pens. There was a tendency for those on the highest scale of rationing to be rather more contented and restful than the restricted pigs. In one or two cases the highest level of feeding appeared to be slightly above the appetite of the pigs, which did not always clear up readily their full allowance of meal.

The health of the pigs was very good. From Table I it will be seen that only seventeen pigs out of the total failed to be despatched to the factory. Of these, eleven were removed from the experiment owing to loss of weight or a practically stationary condition, in some cases resulting from chill, one was ruptured, one contracted erysipelas. There were only two deaths; one of these was from fighting. The remaining two pigs making the total of seventeen were removed simply to balance the experimental design. The seventeen pigs were made up of five from treatment I, five from treatment II and seven from treatment III.

(2) *Rate of live-weight gain.* It has been mentioned that pigs were allowed a "preliminary period" prior to the start of the experimental rationing, and that this covered the period 70–100 lb. live weight. The true experimental period ran from the time pigs were 100 lb., at which weight they were from 4 to 5 months old, to the time when they were despatched to the factory at, or near, 200 lb. live weight, the average age then being about 7 months. During the "preliminary period" they became accustomed to their groups and pens and were eating the meal mixture which was to be fed to them during the true experimental period. Also, pigs which were obviously "poor doers" could be removed and replaced where possible with other pigs. As weekly weighings were made, the rate of progress of the different pens whilst all on the same rations could be measured, and thus their uniformity of performance observed. The rate of live-weight gain over the full experimental period and over the periods 100–140 lb. and 140–200 lb. is shown in Tables III–V.

In these tables the separate results for each centre are given, together with the results of the combined analysis. In the case of Harper Adams College, the results for each separate replication (corresponding to one experiment at the other centres) are given in addition to the combined results for this centre.

With the exception of the "autumn" centres for the period 100–140 lb. the net results show in each case a significantly lower rate of

live-weight gain with increased restriction of feeding. Expressing the rate-of-gain figures as the number of days required to fatten from 100 to 200 lb. live weight, these become:

	Treatment		
	I	II	III
"Summer" group	70·4	75·2	80·6
"Autumn" group	70·9	73·5	77·5

so that pigs on the lowest level took, on the average, 8–10 days longer to reach bacon weight than those on the highest.

Table III. *Rate of live-weight gain per day (lb.).*
Full experimental period

Centre†	Pigs per treat-ment	Treatment means			S.E. of a mean	S.E. of 1 pig as % G.M.	Signifi-cance‡
		I	II	III			
A. "Summer" group:							
N. Ireland	9	1·50	1·30	1·09	0·038	8·98	§Reg.***
Dauntsey's Sch.	6	1·57	1·38	1·30	0·118	20·57	Insig.
Lancs C.C.	8	1·27	1·29	1·40	0·042	9·03	,,
Monmouth F.I.	6	1·34	1·20	1·18	0·026	5·13	Reg.**
Herts	5	—	1·25	1·12	0·058	11·06	Insig.
Kirton	5	1·53	1·45	1·33	0·071	11·06	,,
Harper Adams (A)	5	1·46	1·43	1·25	0·086	13·95	,,
,,　　　　(B)	5	1·51	1·41	1·24	0·036	5·74	Reg.***
Midland	6	1·33	1·30	1·07	0·067	13·39	Reg.*
Newton Rigg	6	1·36	1·31	1·15	0·044	8·39	Reg.**
Durham	6	1·35	1·31	1·48	0·056	10·00	Insig.
All above centres combined (exc. Herts)	62	1·42	1·33	1·24	0·032	18·77	Reg.**
B. "Autumn" group:							
Dauntsey's Sch.	9	1·46	1·24	1·17	0·046	10·83	Reg.***
Hants	7	1·54	1·47	1·30	0·040	7·38	Reg.**
Yorks	5	1·39	1·34	1·14	0·114	19·73	Insig.
Somerset	6	1·70	1·59	1·30	0·078	12·50	Reg.**
Harper Adams (C)	5	1·31	1·31	1·30	0·044	7·54	Insig.
,,　　　　(D)	5	1·17	1·28	1·27	0·094	16·81	,,
,,　　　　(E)	5	1·43	1·34	1·36	0·065	10·61	,,
,,　　　　(F)	4	1·46	1·29	1·36	0·085	12·44	,,
,,　　　　(G)	5	1·30	1·44	1·46	0·053	8·56	,,
,,　　　　(H)	5	1·27	1·30	1·36	0·051	8·70	,,
,,　　　　(C–H combined)	29	1·32	1·33	1·35	0·026	10·66	,,
All above centres combined	56	1·41	1·36	1·29	0·033	18·24	Reg.*
Cheshire	6	1·71	1·46	1·23	0·026	4·34	Reg.***

† The names of the centres given in Table I have been abbreviated for the sake of convenience.

‡　　* =Significant with $P < 0.05 > 0.01$.
　　** =Significant with $P < 0.01 > 0.001$.
　　*** =Significant with $P < 0.001$.

§ Regression term, representing general trend from treatment I to treatment III.

Table IV. *Rate of live-weight gain per day (lb.).*
From start to 140 lb. live weight

Centre	Pigs per treat-ment	Treatment means			S.E. of a mean	S.E. of 1 pig as % G.M.	Signifi-cance
		I	II	III			
A. "Summer" group:							
N. Ireland	9	1·30	1·27	1·07	0·053	13·14	Reg.**
Dauntsey's Sch.	7	1·44	1·56	1·41	0·106	17·68	Insig.
Lancs	8	1·15	1·36	1·31	0·089	19·69	,,
Monmouth	6	1·31	1·23	1·22	0·047	9·08	,,
Herts	5	—	1·22	1·16	0·075	14·14	,,
Kirton	5	1·25	1·20	1·13	0·098	18·35	,,
Harper Adams (A)	5	1·31	1·38	1·19	0·097	16·74	,,
,, (B)	5	1·32	1·21	1·06	0·086	15·98	,,
Midland	6	1·19	1·17	1·08	0·086	18·40	,,
Newton Rigg	6	1·19	1·26	1·16	0·067	13·78	,,
Durham	6	1·15	1·19	1·22	0·065	13·51	,,
All above centres combined (exc. Herts)	63	1·26	1·29	1·19	0·024	15·08	I, II > III**
B. "Autumn" group:							
Dauntsey's Sch.	9	1·14	1·04	1·04	0·049	13·84	Insig.
Hants	7	1·58	1·58	1·47	0·071	12·18	,,
Yorks	5	1·24	1·25	1·12	0·140	25·92	,,
Somerset	6	1·73	1·86	1·36	0·170	25·26	,,
Harper Adams (C)	5	1·24	1·16	1·05	0·083	16·22	,,
,, (D)	5	1·14	1·08	1·21	0·083	16·31	,,
,, (E)	5	1·18	1·16	1·27	0·060	11·21	,,
,, (F)	4	1·31	1·22	1·20	0·027	4·47	Reg.*
,, (G)	5	1·16	1·33	1·33	0·091	16·05	Insig.
,, (H)	5	1·12	1·14	1·23	0·063	12·07	,,
,, (C–H combined)	29	1·19	1·18	1·22	0·033	14·91	,,
All above centres combined	56	1·29	1·29	1·22	0·034	20·20	Insig.
Cheshire	6	1·62	1·45	1·29	0·049	8·20	Reg.***

(3) *Economy of food conversion.* Table VI shows the amount of meal required to produce 1 lb. live-weight gain per pig at the different centres over the two parts of the fattening period and over the whole period 100–200 lb. The statistical analysis of these figures is summarized in Table VII. From these results it is clear that in the group-feeding experiments the pigs on the lowest level of feeding were more efficient than those on the "medium" level, and these again were more efficient than those on the "high" scale; this was the case in both "summer" and "autumn" groups. At Harper Adams, where replication at the centre itself allowed of proper analysis, the same result was obtained. On the other hand, the results from the individually fed pigs at the Cheshire centre showed a trend in the opposite direction. It would appear that for these pigs the level of rationing on the "medium" and "low" scales was below the optimum; other evidence from this centre also

Table V. *Rate of live-weight gain per day (lb.).*
From 140 *lb. live weight to slaughter*

Centre	Pigs per treat- ment	Treatment means I	II	III	s.e. of a mean	s.e. of 1 pig as % g.m.	Significance
A. "Summer" group:							
N. Ireland	9	1·62	1·32	1·09	0·039	8·67	Reg.***
Dauntsey's Sch.	6	1·63	1·30	1·24	0·095	16·82	Reg.*
Lancs	8	1·33	1·24	1·46	0·076	15·98	Insig.
Monmouth	6	1·36	1·15	1·08	0·044	8·99	Reg.**
Herts	5	—	1·28	1·08	0·071	13·51	Insig.
Kirton	5	1·79	1·63	1·47	0·088	12·04	Reg.*
Harper Adams (A)	5	1·61	1·45	1·29	0·097	14·96	Insig.
„ (B)	5	1·64	1·59	1·34	0·039	5·73	Reg.***
Midland	6	1·40	1·41	1·07	0·073	13·83	I, II>III**
Newton Rigg	6	1·51	1·28	1·11	0·066	12·36	Reg.**
Durham	6	1·48	1·40	1·61	0·070	11·51	Insig.
All above centres combined (exc. Herts)	62	1·53	1·36	1·27	0·042	23·74	Reg.***
B. "Autumn" group:							
Dauntsey's Sch.	9	1·63	1·37	1·26	0·063	13·33	Reg.***
Hants	7	1·49	1·40	1·20	0·063	12·12	Reg.**
Yorks	5	1·51	1·42	1·13	0·114	18·80	Reg.*
Somerset	6	1·69	1·50	1·27	0·085	14·00	Reg.**
Harper Adams (C)	5	1·35	1·39	1·53	0·072	11·41	Insig.
„ (D)	5	1·17	1·37	1·33	0·121	20·93	,,
„ (E)	5	1·66	1·47	1·42	0·104	15·37	,,
„ (F)	4	1·58	1·37	1·49	0·164	22·21	,,
„ (G)	5	1·39	1·53	1·54	0·060	9·04	,,
„ (H)	5	1·35	1·42	1·44	0·069	10·96	,,
„ (C–H combined)	29	1·41	1·43	1·45	0·041	15·58	,,
All above centres combined	56	1·49	1·44	1·34	0·042	21·99	Reg.*
Cheshire	6	1·79	1·48	1·19	0·026	4·27	Reg.***

suggests that the pigs require a relatively high level of feeding in order to produce economic gains. It will be noticed from Table VI that the results from the Northern Ireland centre showed a similar trend, but, as this was a group-feeding trial, the significance of these figures cannot be tested.

On the basis of the combined group-feeding figures in Table VI, the average saving in meal, between the "high" and "low" scales, is 39 lb. per pig for the "summer" centres and 73 lb. for the "autumn" centres; the average, over both series of experiments, is thus 56 lb. This agrees well with the figure 51·9 obtained from the recorded food consumption approximately over the period 100–200 lb. live weight in the eleven experiments which were completed without any withdrawals of pigs. These amounts are given in Table VIII.

Table VI. *Lb. food per lb. live-weight gain*

| | Live-weight period | | | | | | | | |
| | 100–140 lb. treatment | | | 140–200 lb. treatment | | | 100–200 lb. treatment | | |
Centre	I	II	III	I	II	III	I	II	III
Summer start:									
N. Ireland	3·44	3·53	3·94	4·03	4·42	4·41	3·78	4·04	4·24
Dauntsey's Sch.	3·36	3·09	3·14	5·10	4·73	4·34	4·27	4·06	3·77
Lancs	4·14	3·25	3·20	5·11	4·95	3·69	4·73	4·23	3·57
Monmouth	3·46	3·47	3·32	5·05	5·26	4·65	4·21	4·34	3·93
Kirton	3·51	3·50	3·87	3·95	3·60	3·39	3·78	3·56	3·56
Harper Adams (A)	3·78	3·28	3·62	4·35	4·17	3·84	4·10	3·87	3·76
,, (B)	3·77	3·87	4·10	4·15	3·75	3·61	4·02	3·80	3·79
Midland	4·00	3·89	3·95	4·72	4·29	4·62	4·46	4·17	4·38
Newton Rigg	4·09	3·64	3·59	4·89	5·18	4·73	4·54	4·39	4·19
Durham	4·42	4·12	4·13	4·89	4·42	3·32	4·72	4·31	3·56
Herts	—	3·56	3·55	—	4·65	4·65	—	4·12	4·14
Autumn start:									
Dauntsey's Sch.	4·48	4·44	4·27	4·36	4·42	4·08	4·39	4·43	4·14
Hants	2·72	2·97	3·00	5·11	4·24	4·14	4·25	3·72	3·67
Yorks	3·58	3·65	3·85	4·51	4·20	4·66	4·12	3·94	4·32
Somerset	2·75	2·51	3·19	4·14	4·06	3·96	3·78	3·63	3·72
Harper Adams (C)	3·78	3·93	4·13	5·11	4·32	3·49	4·66	4·17	3·72
,, (D)	4·32	4·60	3·55	5·95	5·04	4·11	5·35	4·22	3·89
,, (E)	4·09	3·90	3·41	4·24	4·07	3·51	4·18	4·01	3·47
,, (F)	4·29	4·15	3·96	4·60	4·66	3·67	4·49	4·45	3·77
,, (G)	4·29	3·39	3·39	5·02	3·91	3·25	4·72	3·69	3·30
,, (H)	4·27	3·97	3·43	5·13	4·36	3·53	4·85	4·22	3·50
,, (C–H combined)	4·17	3·99	3·65	5·01	4·23	3·84	4·71	4·13	3·61

Table VII. *Lb. food per lb. live-weight gain*

| | Treatment means | | | s.e. of | |
	I	II	III	a mean	Significance
"Summer" group:					
From 100 to 140 lb.	3·80	3·56	3·69	0·07	Insig.
,, 140 to 200 ,,	4·62	4·48	4·06	0·11	Reg.**
,, 100 to 200 ,,	4·26	4·08	3·87	0·08	Reg.**
"Autumn" group:					
From 100 to 140 lb.	3·86	3·75	3·62	0·10	Insig.
,, 140 to 200 ,,	4·82	4·23	3·84	0·14	Reg.***
,, 100 to 200 ,,	4·48	4·05	3·75	0·10	Reg.***
Harper Adams (autumn) combined results:					
From 100 to 140 lb.	4·17	3·99	3·65	0·13	Reg.*
,, 140 to 200 ,,	5·01	4·23	3·84	0·15	Reg.***
,, 100 to 200 ,,	4·71	4·13	3·61	0·10	Reg.***
Cheshire School of Agriculture:					
From 100 to 140 lb.	2·97	3·15	3·32	0·11	Reg.*
,, 140 to 200 ,,	3·89	4·11	4·23	0·07	Reg.**
,, 100 to 200 ,,	3·52	3·75	3·86	0·06	Reg.**

Table VIII. *Average weight of food consumed per pig over period* 100–200 *lb. live weight* (*lb.*)

Centre		Scale of feeding		
		I	II	III
N. Ireland		403·4	422·0	427·0
Kirton		469·2	442·0	390·4
Harper Adams	(A)	431·4	438·4	383·2
„	(B)	427·4	391·2	381·2
Midland		477·7	475·7	460·7
Dauntsey's Sch.		512·7	495·4	426·8
Yorks		511·6	439·2	484·2
Somerset		358·2	339·5	348·8
Harper Adams	(C)	486·0	440·4	391·0
„	(E)	445·8	444·0	370·4
„	(H)	466·6	467·6	355·2
Average		453·6	435·9	401·7

Table IX. *Post-slaughter results; "summer" group of centres*

Variable	No. of pigs per treat-ment	Treatment means			s.e. of a mean	s.e. of 1 pig as % g.m.	Significant treatment differences
		I	II	III			
Final live weight at farm (lb.)	56	210·0	210·4	208·5	—	—	—
Hot carcass weight (lb.)	56	156·3	158·8	157·1	1·30	6·18	—
Hot carcass wt. corrected for final live weight (lb.)	56	*156·1*	*158·2*	*158·0*	*0·77*	*3·66*	—
Dressing %	56	74·4	75·5	75·4	0·35	3·49	II, III > I*
Length of body cavity (mm.)	56	779·5	780·4	782·7	2·41	2·31	—
Depth of carcass (mm.)	56	341·2	344·0	341·2	1·12	2·45	—
Length of leg (mm.)	56	600·5	602·9	605·3	1·99	2·47	—
Length of trotter (mm.)	45	117·8	120·1	120·3	1·26	6·15	—
Weight of trotter (g.)	56	371·2	384·9	388·9	6·58	12·90	—
Weight of flares (g.)	47	1406·7	1401·8	1402·4	49·37	22·57	—
Weight of fillets (g.)	47	445·6	454·3	465·6	7·60	10·71	—
Weight of kidneys (g.)	47	286·7	267·1	261·8	5·96	15·04	Reg.***
Thickness of back-fat A (mm.)	56	50·0	49·6	47·5	0·78	11·91	Reg.*
Back-fat A corrected for carcass (mm.)	56	*50·4*	*48·2*	*47·8*	*0·64*	*9·72*	Reg.**
Thickness of back-fat B (mm.)	56	26·0	25·7	24·6	0·64	18·99	—
Back-fat B corrected for carcass wt. (mm.)	56	*26·4*	*25·2*	*24·7*	*0·49*	*14·50*	Reg.*
Thickness of back-fat C_3 (mm.)	56	34·7	34·2	33·8	0·92	20·02	—
Back-fat C_3 corrected for carcass wt. (mm.)	56	*35·3*	*33·5*	*34·0*	*0·69*	*15·20*	—
Thickness of back-fat C_2 (mm.)	56	31·6	30·4	29·7	0·95	23·39	—
Back-fat C_2 corrected for carcass wt. (mm.)	56	*32·0*	*29·9*	*29·9*	*0·88*	*21·50*	—
Thickness of back-fat C_1 (mm.)	56	38·9	37·6	37·2	1·12	22·20	—
Back-fat C_1 corrected for carcass wt. (mm.)	56	*39·4*	*36·9*	*37·4*	*0·67*	*13·24*	—
Thickness of flank B (mm.)	56	38·6	39·3	39·0	0·53	10·15	—
Refractive index of back-fat† (exc. N. Ireland and Herts)	47	53·81	53·86	53·99	—		

† See note, Table XII.

B. *Post-slaughter results.*

Tables IX and X summarize the post-slaughter records for the "summer" and "autumn" groups of experiments respectively (excluding the Hertfordshire centre, and the first experiment at Dauntsey's School),

Table X. *Post-slaughter results; "autumn" group of centres*

Variable	No. of pigs per treatment	Treatment means			s.e. of a mean	s.e. of 1 pig as % G.M.
		I	II	III		
Final live weight at farm (lb.)	56	209·7	208·6	206·8	—	—
Hot carcass weight (lb.)	56	155·7	155·3	154·3	0·99	4·76
Hot carcass wt. corrected for final live weight (lb.)	*56*	*154·8*	*155·1*	*155·3*	*0·54*	*2·59*
Dressing %	56	74·3	74·5	74·5	0·24	2·38
Length of body cavity (mm.)	56	766·1	765·7	767·2	2·30	2·25
Depth of carcass (mm.)	56	342·5	341·6	342·6	1·50	2·38
Length of leg (mm.)	56	585·7	583·7	589·3	2·17	2·39
Length of trotter (mm.)	56	118·2	118·0	119·4	0·79	4·93
Weight of trotter (g.)	47	368·0	371·9	371·6	4·14	7·11
Weight of flares (g.)	51	1360·8	1391·0	1309·8	44·36	23·40
Weight of fillets (g.)	56	457·1	452·7	464·2	7·97	13·02
Weight of kidneys (g.)	56	278·6	271·1	266·7	3·84	10·58
Thickness of back-fat A (mm.)	56	47·3	46·9	46·2	0·65	10·40
Back-fat A corrected for carcass wt. (mm.)	*56*	*47·0*	*46·8*	*46·6*	*0·50*	*8·07*
Thickness of back-fat B (mm.)	56	23·6	23·8	23·4	0·54	17·02
Back-fat B corrected for carcass wt. (mm.)	*56*	*23·4*	*23·7*	*23·8*	*0·39*	*12·28*
Thickness of back-fat C_3 (mm.)	56	33·5	34·0	32·8	0·56	12·57
Back-fat C_3 corrected for carcass wt. (mm.)	*56*	*33·3*	*33·9*	*33·1*	*0·45*	*10·16*
Thickness of back-fat C_2 (mm.)	56	29·3	29·2	28·2	0·68	17·75
Back-fat C_2 corrected for carcass wt. (mm.)	*56*	*29·0*	*29·1*	*28·5*	*0·55*	*14·20*
Thickness of back-fat C_1 (mm.)	56	38·0	38·3	36·6	0·88	17·43
Back-fat C_1 corrected for carcass wt. (mm.)	*56*	*37·6*	*38·2*	*37·1*	*0·64*	*12·71*
Thickness of flank B (mm.)	56	33·5	34·0	33·4	0·37	8·31
Refractive index of back-fat*	56	53·70†	53·83†	54·19†	0·16	2·22

There were no significant treatment differences apart from those shown in the refractive index.

     * See note, Table XII.   † Regression significant, $P < 0.05$.

and Table XI gives the results at the Cheshire centre. These tables show that, on the average, the effects of the different scales of rationing on carcass conformation were only slight. In Table IX increased restriction of feeding is shown to have produced significantly lower kidney weight, and slight, but significant, reductions in the back-fat thickness over the shoulder and at the middle of the back, after correction has been made for differences in carcass weight. There is no appreciable effect on the unsaturation of the back-fat, as reflected in the refractive index. Dressing percentage has increased slightly with limitation of the ration. In the

"autumn" group of centres (Table X), no significant effects at all are to be noted, with the exception of an increase in the unsaturation of the back-fat (significant with $P < 0.05$), as shown by the refractometer readings. In the individual feeding experiment at Cheshire (Table XI)

Table XI. *Post-slaughter results; Cheshire School of Agriculture*

Variable	Treatment means			s.e. of a mean	s.e. of 1 pig as % G.M.	Significant treatment differences
	I	II	III			
Final live weight at farm (lb.)	200·2	208·8	198·2	2·056	2·49	Insig.
Hot carcass weight (lb.)	153·2	162·0	155·6	1·797	2·81	,,
Hot carcass wt. corrected for final live weight (lb.)	*154·5*	*157·9*	*158·2*	*1·237*	*1·93*	,,
Dressing %	76·5	77·9	78·5	0·563	1·78	Reg.*
Length of body cavity (mm.)	789·0	798·3	783·3	6·533	2·02	Insig.
Depth of carcass	340·3	343·2	340·3	4·221	3·03	,,
Length of leg (mm.)	595·1	616·8	599·8	4·455	1·81	II > I, III*
Length of trotter (mm.)	112·0	117·0	117·8	2·878	6·09	Insig.
Weight of trotter (g.)	334·5	378·5	396·0	15·624	10·35	Reg.*
Weight of flares (g.)	1243·6	1694·5	1591·6	170·533	27·67	Insig.
Weight of fillets (g.)	463·3	492·2	451·0	13·158	6·88	,,
Weight of kidneys (g.)	276·0	259·6	235·0	6·458	6·16	Reg.**
Thickness of back-fat A (mm.)	53·2	50·3	48·8	1·703	8·21	Insig.
Thickness of back-fat B (mm.)	25·5	23·5	23·3	1·374	13·96	,,
Back-fat B corrected for carcass wt. (mm.)	*27·9*	*20·1*	*24·1*	*0·750*	*7·62*	*I > II, III** III > II**
Thickness of back-fat C_3 (mm.)	33·2	33·2	29·8	1·396	10·67	Insig.
Thickness of back-fat C_2 (mm.)	29·3	27·3	25·7	1·401	12·51	,,
Thickness of back-fat C_1 (mm.)	36·7	34·2	30·3	1·742	12·65	Reg.*
Thickness of flank B (mm.)	33·8	38·5	39·0	1·731	11·43	Insig.
Refractive index of back-fat†	52·60	53·98	55·05	—	2·34	Reg.**

† See note, Table XII.

the carcass records again show an increase in dressing percentage, and a decrease in kidney weight through restriction, with a tendency for the thickness of the middle back-fat and rump-fat to be reduced slightly; the back-fat is again rather more unsaturated in the pigs on the restricted rations. It should be mentioned that this effect on the back-fat was in all cases only slight, no cases of actually "soft" fat being reported, but the sensitivity of the method of examination employed has allowed relatively small differences to be detected. The results for the different centres are individually shown in Table XII.

In Table XIII are shown the average values, over all treatments, for various carcass records at the different centres. This shows the very considerable variation met with from centre to centre in any given record. The methods of obtaining the records were standardized as far as possible, and, whilst some of the variation is no doubt due to differences in the weight at which pigs were slaughtered, and to transit effects, it is clear that a portion at least is ascribed to differences in conformation of the

Table XII. *Refractive index of back-fat*†

Centre	No. of pigs per treatment	Treatment means I	II	III	S.E. of a mean	S.E. of 1 pig as % G.M.	Significant treatment differences
N. Ireland‡	9	63·32	64·14	66·04	0·47	2·20	Reg.***
Lancs	8	53·43	53·88	52·87	0·31	1·65	—
Monmouth	6	52·54	53·36	53·96	0·36	1·65	Reg.*
Kirton	5	52·69	52·24	51·80	0·50	2·12	Reg.*
Harper Adams (A)	5	56·31	54·66	55·50	0·57	2·32	—
„ (B)	5	54·91	55·20	55·10	0·30	1·23	—
Midland	6	53·93	55·10	55·51	0·65	2·91	—
Newton Rigg	6	54·44	52·78	54·48	0·19	0·85	I, III > II***
Durham	6	52·74	53·76	53·12	0·37	1·70	—
Herts	5	—	52·23	54·58	1·03	4·33	—
Above centres combined§	47	53·81	53·86	53·99	—	—	—
Dauntsey's Sch.	9	53·31	54·32	54·88	0·41	2·30	Reg.*
Hants	7	53·19	53·32	53·52	0·31	1·54	—
Yorks	5	53·66	54·02	54·33	0·36	1·51	—
Somerset	6	52·71	53·98	53·81	0·43	1·95	—
Harper Adams (C)	5	53·64	53·86	54·47	0·26	1·08	—
„ (D)	5	54·99	54·75	54·17	0·27	1·11	—
„ (E)	5	54·04	53·64	53·90	0·75	3·11	—
„ (F)	4	53·41	53·80	54·04	0·57	2·11	—
„ (G)	5	54·12	52·80	54·27	0·30	1·24	I, III > II**
„ (H)	5	54·61	53·54	54·22	0·25	1·02	I > II*
„ (C–H combined)	29	54·16	53·73	54·19	0·19	1·80	—
Above centres combined	56	53·70	53·83	54·19	0·16	2·22	Reg.*
Cheshire	6	52·60	53·98	55·05	0·51	2·34	Reg.**

† The figures given are refractometer scale readings (kindly supplied by the Low Temperature Research Station, Cambridge). They may be converted into absolute refractive indices by taking a reading of 50·00 as equivalent to a refractive index of 1·45907, and one of 56·00 as 1·46063, with linear interpolation, but for purposes of comparison are more useful as given.

‡ Iodine values (kindly supplied by Prof. Baskett).

§ Excluding N. Ireland and Herts.

different breeds and strains used. The values for the ratio of thickness of shoulder-fat to thickness of middle back-fat (A : B) are of interest in pointing towards differences in maturity of the pigs utilized; low values of this ratio may be considered as indicative of a relatively advanced state of maturity (Hammond & Murray, 1937). It has been suggested that pigs of the early maturing type, which tend to put on more fat at any one weight, will have to be limited in their ration more and at an earlier age than will later maturing pigs in order to obtain the optimum results (Hammond & Murray, 1937). Space prevents the presentation of the full data of carcass records for the different centres, but the results for shoulder-fat and middle back-fat measurements are given in Tables XIV and XV. It will be seen that the extent of the response to

Table XIII. *Mean values of various carcass records at each centre*

Centre	Final live weight at farm lb.	Hot carcass weight lb.	Length of body cavity mm.	Depth of carcass mm.	Length of leg mm.	Thickness of back-fat A mm.	Thickness of back-fat B mm.	Ratio A/B	Av. thickness of rump fat (C_2, C_3, C_1) mm.	Thickness of belly mm.
N. Ireland	203·6	155·5	771·5	344·3	618·8	49·8	26·4	1·89	35·6	31·5
Lancs	206·9	157·5	793·5	336·7	596·8	50·4	25·2	2·00	33·0	37·8
Monmouth	208·4	158·7	765·6	354·8	600·5	57·1	30·5	1·87	41·8	42·4
Kirton	209·7	154·7	796·0	347·3	605·8	53·0	26·4	2·01	37·4	30·0
Harper Adams (A)	210·1	155·3	772·3	334·6	581·3	42·3	22·1	1·91	29·9	43·1
,, (B)	207·9	151·6	773·1	329·6	585·0	41·7	21·8	1·91	29·6	40·2
Midland	210·1	157·5	795·7	345·4	612·4	43·5	23·5	1·85	31·0	42·5
Newton Rigg	209·4	158·5	788·2	337·9	602·7	50·1	24·8	2·02	32·0	43·5
Durham	222·9	166·8	772·1	346·8	610·9	51·2	26·8	1·91	36·7	43·7
Herts	208·3	155·5	770·6	339·0	604·1	51·2	24·0	2·13	32·5	25·5
Dauntsey's Sch.	215·4	159·3	791·0	344·8	609·0	48·9	23·1	2·12	32·3	28·2
Hants	204·3	157·0	782·8	345·6	600·7	52·2	24·9	2·10	33·7	29·2
Yorks	205·7	152·3	763·6	347·5	592·4	48·1	25·5	1·89	34·2	30·9
Somerset	204·9	153·8	763·1	343·9	586·3	51·2	27·3	1·87	39·3	41·3
Harper Adams (C)	208·9	154·3	760·3	338·2	578·3	44·3	22·3	1·99	32·0	34·9
,, (D)	211·3	157·7	759·2	341·9	575·2	42·8	22·5	1·90	31·3	37·9
,, (E)	208·4	153·2	751·7	337·9	571·5	45·1	24·3	1·85	34·2	33·7
,, (F)	208·5	154·0	764·0	333·6	580·4	42·1	22·1	1·90	32·0	34·2
,, (G)	206·1	152·9	750·8	337·4	574·3	44·6	21·7	2·05	31·0	34·5
,, (H)	207·0	152·4	750·5	346·3	569·2	43·3	21·3	2·03	32 3	36·6
,, (C–H combined)	208·3	154·1	755·8	339·4	574·6	43·8	22·4	1·95	32·1	35·3
Cheshire	202·3	156·8	790·2	341·3	603·9	50·8	24·1	2·11	30·9	37·2

restriction as reflected in these figures varies with the centres, but the general trend is clearly in the direction of that obtained by the combined results. The estimate of experimental error is also seen to vary considerably from centre to centre. In Table XV the result for Lancashire is certainly anomalous, but is probably explained by the fact that the pigs at this centre were killed at average weights of approximately 204, 206, 211 lb. under treatments I, II and III respectively. A significant value of the correlation coefficient between back-fat thickness and live weight or carcass weight, to allow due correction to be made, could not be obtained, however, from the data at this centre. No clear relation can be found between the responses shown in Tables XIV and XV and the average carcass characteristics referred to in Table XIII. A connexion might also be sought, perhaps, between the reduction in back-fat thickness due to restricted feeding and the corresponding reduction in rate of live-weight increase. Comparison of the size of the treatment effect in Tables XIV and XV with the extent of the reduction in rate of live-weight gain shown in Tables III and V does not bring out any

Table XIV. *Thickness of shoulder-fat (A) at each centre (mm.)*

Centre	No. of pigs per treatment	Treatment means I	II	III	S.E. of a mean	S.E. of 1 pig as % G.M.	Significant treatment differences
N. Ireland	9	51·8	49·9	47·7	1·13	6·83	Reg.*
Lancs	8	49·1	49·5	52·5	1·54	8·65	—
Monmouth	6	60·8	58·5	51·8	2·16	9·27	Reg.*
Kirton	5	51·7	54·9	52·5	1·58	6·65	—
Harper Adams (A)	5	42·8	42·4	41·6	1·53	8·09	—
„ (B)	5	43·4	42·0	39·8	1·51	8·12	—
Midland	6	44·0	44·8	41·7	1·64	9·23	—
Newton Rigg	6	50·5	54·0	45·8	1·09	5·33	I>III*, II>III**
Durham	6	53·3	49·0	51·3	1·47	7·02	—
Herts	5	—	52·6	49·8	1·51	6·58	—
All above centres combined (exc. Herts)	56	50·0	49·6	47·5	0·78	11·91	Reg.*
Combined results corrected for carcass wt.	56	50·4	48·2	47·8	0·64	9·72	Reg.**
Dauntsey's Sch.	9	51·8	48·8	46·0	1·91	11·70	†Reg.*
Hants	7	53·7	51·7	51·1	1·16	5·89	
Yorks	5	48·2	46·0	50·0	2·28	10·61	
Somerset	6	50·2	50·0	53·3	1·78	8·54	
Harper Adams (C)	5	44·6	43·2	45·0	0·87	4·37	
„ (D)	5	43·8	44·0	40·6	2·32	12·11	
„ (E)	5	44·0	45·8	45·6	1·49	7·39	
„ (F)	4	43·3	41·5	41·5	2·36	11·23	
„ (G)	5	44·2	48·2	41·4	2·01	10·10	
„ (H)	5	42·0	45·2	42·8	1·11	5·72	
„ (C–H combined)	29	43·6	44·6	42·8	0·73	9·15	
All above centres combined	56	47·3	46·9	46·2	0·65	10·40	
Combined results corrected for carcass wt.	56	47·0	46·8	46·6	0·50	8·07	
Cheshire	6	53·2	50·3	48·8	1·70	8·21	

† Insig. when corrected for carcass weight.

close correlation between the two, however, except for the fact that at those centres where a significant reduction in back-fat thickness was obtained, a significant reduction in rate of live-weight gain was also apparent. The reverse of this statement does not appear to hold, i.e. not all centres where rate of gain was decreased show a significant decrease in back-fat thickness. Possibly further correlation studies on the data may bring to light some more definite relationships.

No differential effect of restricted feeding according to the sex of the pigs was obtained. The design of the experiment at the Midland Agricultural College was such that this point could be investigated.

Table XV. *Thickness of mid-back-fat (B) at each centre (mm.)*

Centre	No. of pigs per treatment	Treatment means			s.e. of a mean	s.e. of 1 pig as % g.m.	Significant treatment differences
		I	II	III			
N. Ireland	9	26·5	27·2	25·5	0·58	6·55	—
Lancs	8	23·6	24·1	28·0	0·92	10·30	Reg.**
Monmouth	6	33·3	31·2	27·0	1·62	12·98	†Reg.*,
Kirton	5	27·1	25·2	26·9	1·54	13·07	—
Harper Adams (A)	5	22·6	22·6	21·2	1·62	16·40	—
„ (B)	5	23·4	21·6	20·4	1·19	12·19	—
Midland	6	24·2	23·5	22·8	0·77	8·06	—
Newton Rigg	6	25·8	27·7	20·8	1·51	14·96	I, II>III*
Durham	6	27·0	26·7	26·7	0·80	7·29	—
Herts	5	—	25·6	22·4	0·85 ·	7·91	—
All above centres combined (exc. Herts)	56	26·0	25·7	24·6	0·64	18·99	—
Combined results corrected for carcass wt.	56	26·4		24·7	0·49	14·50	Reg.*
Dauntsey's Sch.	9	24·6	23·2	21·6	1·05	13·69	
Hants	7	26·3	24·0	24·4	1·29	13·70	
Yorks	5	24·4	26·2	26·0	1·11	9·70	
Somerset	6	26·3	26·2	29·3	0·97	8·74	
Harper Adams (C)	5	22·6	21·0	23·2	1·40	14·74	
„ (D)	5	21·2	23·2	23·0	1·96	19·55	
„ (E)	5	22·2	25·8	25·0	1·97	18·09	
„ (F)	4	25·0	20·2	21·0	1·66	15·01	
„ (G)	5	21·4	23·6	20·0	1·80	18·63	
„ (H)	5	20·0	23·6	20·4	1·10	11·49	
„ (C–H combined)	29	22·1	22·9	22·1	0·76	19·24	
All above centres combined	56	23·6	23·8	23·4	0·54	17·02	
Combined results corrected for carcass wt.	56	23·4	23·7	23·8	0·39	12·28	
Cheshire	6	25·5 ·	23·5	23·3	1·37	13·96	

† Insig. when corrected for carcass weight.

Conclusions

From the review of past work which has been given earlier it would appear that there is considerable evidence in support of restricting feeding below the amount needed fully to satisfy appetite; but clearly this must not be carried to such a degree that it becomes uneconomic. In the series of experiments which have now been reported the rate of live-weight gain on even the lowest scale followed can scarcely be regarded as unsatisfactory. Furthermore this level of rationing produced on the average a reduction in meal consumption, and, whilst there is little to choose between the three scales of feeding compared, in so far as carcass quality is concerned, what slight advantage there is, is on the side of the lowest scale. The question is how far the slight advantages resulting from

restricted feeding compensate for the rather longer time required to fatten the pigs under such a system of feeding. The answer to this must depend on the particular circumstances at each establishment where fattening is carried out. Under normal conditions where meals are plentiful and relatively cheap, quickness of turnover is probably of most importance so as to keep overhead and labour expenses per pig at a minimum. If, on the other hand, meal supply is limited, and there is no very heavy demand on labour or accommodation, the most economic utilization of the available food may well carry most weight. Under such conditions, a maximum daily allowance of 5–5½ lb. meal at 170–180 lb. weight would seem to be indicated by the results of the experiments which have been described.

According to recent work (McMeekan & Hammond, 1939; Callow, 1939) feeding should not be restricted before an age of some 16 weeks is reached if satisfactory carcasses are to be produced. Pigs fed on a high plane up to this time, and subsequently restricted, produce good carcasses, but initial restriction, followed by relatively high feeding, gives rise to carcasses of very inferior quality, with excessively thick back-fat and poorly developed muscle.

During the course of the enquiry into the effects of restricted feeding, a questionnaire was circulated to experimental centres in Great Britain, from which it was hoped to gain information on the methods of feeding bacon pigs in common practice. From an analysis of the replies received it would appear that at most centres pigs are rationed on a basis of age, rather than on weight. The amount of food allowed reaches a maximum of 5½–6 lb. per head daily at most of the institutes covered by the questionnaire, and this figure is attained in the region of 160–180 lb. live weight. At some centres, however, the maximum was as high as 7–7½ lb.

It would seem, therefore, that the scale indicated by the results of the trials which are reported here is one which approximates to that followed by many pig-experiment centres. It is likely, however, that in general practice it is usually very considerably exceeded, probably the commonest method of rationing being to allow the pigs as much as they will readily clear up in a given time, regardless of the relation this bears to any quantitative scale of feeding.

SUMMARY

The results are described of twenty-two experiments carried out on the feeding of bacon pigs at different centres throughout Great Britain, in the course of which nearly 400 pigs were fed according to three different scales of rationing. All the pigs were fed on the same scale until reaching 100 lb. live weight, when they were eating 4 lb. of meal per head per day. From this stage three different levels of feeding were followed; in each case the daily allowance reached a maximum when the pigs were 170 lb. live weight. The amounts being fed were then: 7 lb. 8 oz., 6 lb. 5 oz. and 5 lb. 3 oz. per head per day respectively.

Within the range of feeding utilized in these experiments, the following conclusions, based on the average results, can be drawn. 'It is clear, however, that these are liable locally to some modification:

(*a*) Restriction of feeding leads to a slower rate of live-weight gain, involving, on the lowest of the three scales practised, an average increase of 8–10 days in the time required to raise the live weight from 100 to 200 lb.

(*b*) Restriction of feeding tends, on the average, to give a better economy of food conversion, the mean saving in these experiments, between the highest and the lowest scales of feeding, being about 50 lb. of meal per pig over the period 100 lb. to 200 lb. live weight.

(*c*) Restriction according to the scales used in these experiments has, on the average, little effect on carcass quality, except for a tendency towards the production of slightly thinner and softer back-fat.

(*d*) From the experimental results, and from other evidence reviewed here, it would seem that an allowance of about 5–5½ lb. of meal daily, at a live weight of 170–180 lb., is indicated as an economic maximum.

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REFERENCES

BALLINGER, C. E. (1938). *N.Z. J. Agric.* **56**, 299.
BASKETT, R. G., HALE, R. W. & GRAY, G. L. (1937). *J. Minist. Agric. N. Ire.* **5**, 1.
BIGGAR, W. A. (1937). *Pig Breed. Annu.* **17**, 136.
BLISSETT, A. H. (1935). *Pig Breed. Annu.* **15**, 124.
Bull. Bacon Development Bd (1938), no. 3.
CALLOW, E. H. (1935). *Emp. J. exp. Agric.* **3**, 80.
—— (1939). *Rep. Food Invest. Bd., Lond. for* 1938, 45.
CHESHIRE SCH. AGRIC. (1938). *Pig Breed. Annu.* **18**, 131.
CRAMPTON, E. W. (1935). *Sci. Agric.* **15**, 463.
—— (1939). *Sci. Agric.* **19**, 736.
CROWTHER, C. (1937). *Pig Breed. Annu.* **17**, 125.
CROWTHER, C. & HEAP, L. H. (1938). *Pig Breed. Annu.* **18**, 121.
ELLIS, N. R. & ZELLER, J. H. (1931). *Proc. Amer. Soc. anim. Prod.* **270**.
—— ——— (1934). *Tech. Bull. U.S. Dep. Agric.* **413**.
FERRIN, E. F. & McCARTY, M. A. (1928). *Bull. Minn. agric. Exp. Sta.* **248**.
FISHWICK, V. C. (1936). *J. Minist. Agric.* **43**, 235.
FREEMAN, V. A. (1935). *Quart. Bull. Mich. agric. Exp. Sta.* **17**, 95.
HAMMOND, J. (1932). *J. R. agric. Soc.* **93**, 131.
HAMMOND, J. & MURRAY, G. N. (1937). *J. agric. Sci.* **27**, 394.
HUTHNANCE, S. L. & CAMPION, J. E. (1936). *Pig Breed. Gaz.* **36**, 71.
LINDGREN, H. A., OLIVER, A. W. & POTTER, E. L. (1932). *Bull. Ore. agric. Exp. Sta.* **297**.
MANSFIELD, W. S. & TREHANE, W. R. (1935). *J. R. agric. Soc.* **96**, 137.
—— —— (1937). *J. R. agric. Soc.* **98**, 172.
McMEEKAN, C. P. & HAMMOND, J. (1939). *J. Minist. Agric.* **46**, 238.
MIDLAND AGRIC. COLLEGE (1938). *Pig Breed. Annu.* **18**, 136.
Rep. Rothamsted exp. Sta. (1935).
SAINT-PIERRE, J. M., MORRISON, F. B. & WILLMAN, J. P. (1934). *Proc. Amer. Soc. anim. Prod.* **101**.
SHORROCK, R. W. (1940). *Emp. J. exp. Agric.* **8**, 159.
SNEDECOR, G. W. (1938). *Statistical Methods.* Ames, Iowa.
WOOD, T. B. (1927). *Misc. Publ. Minist. Agric. Fish., Lond.,* no. 32.
YATES, F. (1933). *Emp. J. exp. Agric.* **1**, 129.
YATES, F. & COCHRAN, W. G. (1938). *J. agric. Sci.* **28**, 556.

FACTORS AFFECTING THE STABILITY AND ESTIMATION OF CAROTENE IN ARTIFICIALLY DRIED GRASS AND HAYS

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(With Three Text-figures)

INTRODUCTION

IN animal foodstuffs vitamin A is mostly present in the form of the several active carotenoids (α, β, γ carotene and kryptoxanthin) which function as provitamin A. These substances, of which β carotene is the most important are, as is well known, labile. As naturally present in vegetable tissue they are largely protected from destruction. However, in the preparation of animal fodders from plants they are exposed to a combination of factors including heat, light, atmospheric oxygen, etc., with resulting loss of potency.

In a previous paper by Bartlett *et al.* (1938), the effect of different methods of drying on the carotene content of grass has been discussed. Subsequently, the effect of storage on these dried grasses has been investigated. The material which was not ground was stored in the form of pressed bales. In addition, the effect of storage on artificially dried grass which had been ground to a powder has also been studied. Such material must be kept in suitable containers, and it was of interest to find out whether the type of container influences the rate of decomposition of the carotene. Two types of containers, jute and paper sacks, are available commercially for the storage of ground artificially dried grass and both were used. The results of these investigations are described below under three headings. The first deals with the effect of storage under different conditions on the carotene content of artificially dried grass and hay, the second with methods of estimating carotene, and under the third the application of chromatographic analysis to carotene estimations in fodders is discussed.

✦ ·

PART I. EFFECT OF STORAGE UNDER DIFFERENT CONDITIONS ON THE
CAROTENE CONTENT OF ARTIFICIALLY DRIED GRASS AND HAYS

A. LOSS ON STORAGE OF CAROTENE IN GROUND
ARTIFICIALLY DRIED GRASS

(1) *Treatment*

High-quality artificially dried grass was obtained from Derbyshire
in August 1938; this material had been dried in a Ransome-Davies drier,
ground to a fine powder and bagged in ½ cwt. paper sacks on 19 August;
it appeared to be a very even sample, having all been cut from one field.
The analysis supplied by the makers showed a carotene content of
600 mg./kg. and a protein content of 16%. Fifty-two of these sacks
were emptied alternately into twenty-seven plain paper sacks and twenty-
five jute sacks both of good commercial quality. They were fastened with
wire ties, put on a lorry immediately and off-loaded at Shinfield on
24 August. A sample was taken from the mixed contents of one paper
sack and one jute sack, and analysed the same day for moisture and
carotene content.

Half the paper sacks and half the jute sacks were placed in the farm
buildings in a room with an open doorway facing north-west, and the
other half in a dark room with closed doors. The sacks were arranged in
six rows of four, two paper and two jute in each row, thereby equalizing
the conditions of storage within each treatment. The sacks stood on
a dry concrete floor.

For simplicity these two treatments are referred to as (*a*) "Light"
storage, i.e. in the open room where the sacks were exposed to all the
external variations except to wind and rain, and (*b*) "Dark" storage,
i.e. the dark room. A record was kept of the daily maximum and
minimum temperature throughout the six months' storage period.

Later the effect of storage at higher temperatures was also studied.
The material used for this purpose was from sacks previously sampled
in the comparison of "light" versus "dark" storage. The contents of
six paper and six jute sacks were thoroughly mixed in a batch mixer.
The grass was bagged alternately in jute sacks and plain paper sacks
and a sample taken for analysis during the filling. Three paper and three
jute sacks were placed on a dry concrete floor in a heated room, which
was maintained at 70–80° F. by a Halliday gas boiler, only the radiators
being in the room; this treatment is referred to as "summer" storage.
The other six sacks were stored in the open room with the "light"

storage sacks; there the average daily temperature in December and January when the experiment was carried out was around 40° F. This treatment is referred to as "winter" storage.

(2) *Methods of analysis*

For analysis the contents of two paper or jute sacks were mixed thoroughly on a dry concrete floor and from different parts of the heap small handfuls were taken, mixed and placed in a Kilner jar.

Carotene was estimated at first by the method of Ferguson & Bishop (1936), and later parallel determinations were carried out by the method of Peterson, Hughes & Freeman (1937).

Unless specifically stated the conventional nomenclature is used in this paper, i.e. "carotene" refers to the epiphasic and "xanthophyll" to the hypophasic pigments in the phase separation.

Tests were carried out at monthly intervals and moisture determinations were made on all the samples taken.

(3) *Results*

Moisture content.

(a) *"Light" versus "dark" storage.* The initial moisture content (Fig. 1a and Table I) of 4·4 % shows that this grass had been dried very thoroughly. This is apparently necessary to avoid wet patches. On storage there is a rise in the moisture content, at first very rapid, then gradually slowing up as the moisture content approached the maximum at which an equilibrium exists with the relative humidity of the atmosphere.

Table I. *Variation in the moisture content of artificially dried grass stored in paper sacks (plain) and jute sacks, under different conditions*

Date	"Light" storage Paper %	Jute %	"Dark" storage Paper %	Jute %	Date	"Winter" storage Paper %	Jute %	"Summer" storage Paper %	Jute %
24 Aug.	4·4	4·4	4·4	4·4					
21 Sept.	9·8	8·9	8·4	8·4					
17 Oct.	10·6	10·4	8·6	9·4					
21 Nov.	12·2	12·2	10·4	10·3					
19 Dec.	13·0	11·6	10·4	10·5	7 Dec.	12·3	12·3	12·3	12·3
11 Jan.	13·8	12·3	10·8	11·0	10 Jan.	14·4	14·0	7·8	9·5
8 Feb.	13·9	12·8	11·0	11·5	8 Feb.	14·6	14·6	8·4	10·3
Mean	11·1	10·4	9·1	9·4		13·8	13·6	9·5	10·7

The rise was more pronounced and reached a higher level in those sacks stored in the open room and there the paper sacks appeared to have

picked up more moisture than the jute sacks during December, January and February. In the dark store, however, the moisture content in the two sets of sacks ran closely parallel.

(b) *"Winter" versus "summer" storage.* Fig. 1b and Table I show that the initial moisture content after mixing on 6 December was 12·3%;
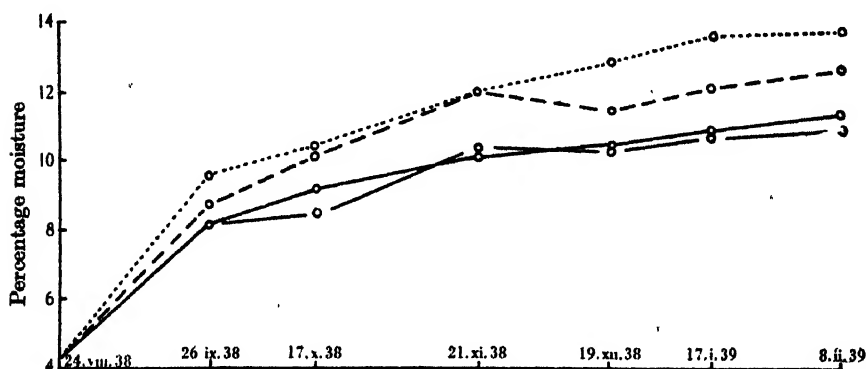

Fig 1 a. Moisture content of artificially dried grass stored in paper and jute sacks in the light and in the dark.

o ·······o Paper sacks⎰ "Light"   o ————o Paper sacks⎰ "Dark"
o — — —o Jute „ ⎰ storage   o ————o Jute „ ⎰ storage
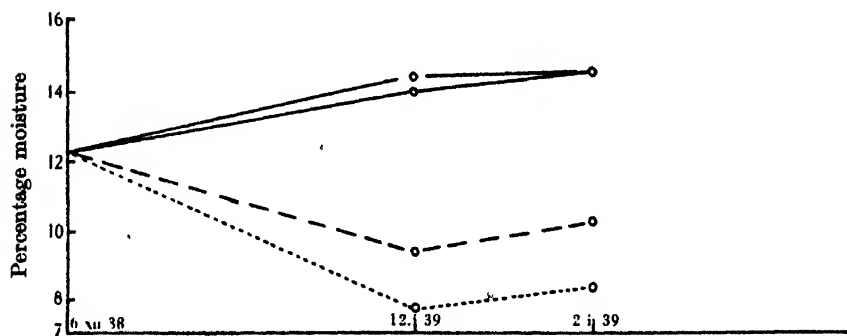

Fig. 1 b. Moisture content of artificially dried grass stored in paper and jute sacks at "summer" and "winter" temperatures.

o ·······o Paper sacks⎰ "Summer"   o ————o Paper sacks⎰ "Winter"
o — — —o Jute „ ⎰ storage   o ————o Jute „ ⎰ storage

under "winter" storage this gradually rose to 14·6%, there being no difference between the two types of sacks. Under "summer" storage, the moisture content fell and then rose slightly. The paper sacks apparently lost moisture more readily than the jute sacks.

Carotene content.

(a) *"Light" versus "dark" storage.* Carotene estimations were carried out by the methods already described. The results are given in Table II

Table II. *Variation in the carotene content of artificially dried grass, stored in paper sacks (plain) and jute sacks, under different conditions*

Carotene expressed as mg./100 g. of dry matter. F.B. = method of Ferguson & Bishop; P. = method of Peterson, Hughes & Freeman

Date		"Light" storage		"Dark" storage		Date		"Winter" storage		"Summer" storage	
		F.B.	P.	F.B.	P.			F.B.	P.	F.B.	P.
24 Aug.	Paper	61·1	—	61·1	—						
	Jute	61·1	—	61·1	—						
21 Sept.	Paper	45·7	38·4	46·6	45·7						
	Jute	49·5	39·9	44·1	42·8						
17 Oct.	Paper	40·5	38·0	47·3	44·0						
	Jute	41·0	41·0	46·4	46·2						
21 Nov.	Paper	45·2	41·6	47·8	44·2						
	Jute	46·8	39·1	47·7	45·0						
19 Dec.	Paper	44·2	—	47·9	—	7 Dec.	Paper	42·9	—	42·9	—
	Jute	41·9	—	51·0	—		Jute	42·9	—	42·9	—
11 Jan.	Paper	44·0	41·3	42·3	44·4	12 Jan.	Paper	42·5	41·6	41·8	37·7
	Jute	46·2	38·3	43·0	44·4		Jute	44·5	42·8	46·8	39·3
8 Feb.	Paper	46·4	36·8	38·9	36·1	8 Feb.	Paper	43·7	37·1	38·2	34·8
	Jute	41·6	36·0	40·7	36·4		Jute	45·9	38·1	37·5	35·2
Mean	Paper	46·7	39·2	47·4	42·9			43·0	39·4	41·0	36·3
	Jute	46·9	38·9	47·7	43·0			44·4	40·5	42·4	37·3

Fig. 2 *a*. Carotene content of artificially dried grass stored in paper and jute sacks in the light and in the dark estimated by the method of Ferguson & Bishop.

o · · · · · · · o Paper sacks ⎫ "Light"   o ———— o Paper sacks ⎫ "Dark"
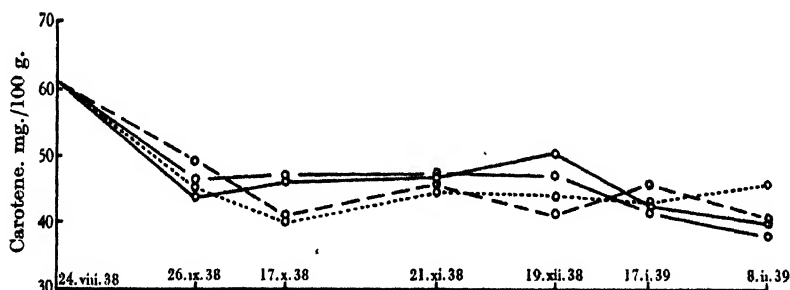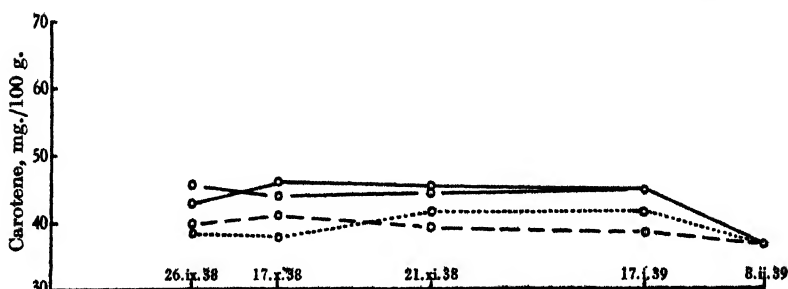o — — — o Jute   „   ⎭ storage   o————o Jute   „   ⎭ storage

Fig. 2 *b*. Carotene content of artificially dried grass stored in paper and jute sacks in the light and in the dark estimated by the method of Peterson *et al.*

o · · · · · · · o Paper sacks ⎫ "Light"   o ———— o Paper sacks ⎫ "Dark"
o — — — o Jute   „   ⎭ storage   o————o Jute   „   ⎭ storage

and Fig. 2 a, b. The initial carotene content was 61·1 mg./100 g. This is in close agreement with the carotene content for the bulk sample quoted by the suppliers.

The carotene content decreased by 23·9 % during the first month's storage (24 August–21 September). From September to February there was a further loss of 7·5 %; no difference, however, could be detected between the plain paper sacks and the jute sacks. The method of Peterson, Hughes & Freeman (1937) gave slightly lower values than the method
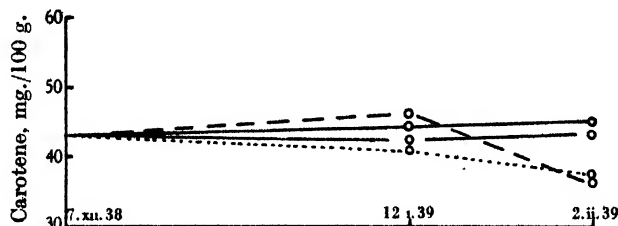

Fig. 3 a. Carotene content of artificially dried grass stored in paper and jute sacks at "summer" and "winter" temperatures estimated by the method of Ferguson & Bishop.

o······o Paper sacks ⎱ "Summer"   o———o Paper sacks ⎱ "Winter"
o— — —o Jute ,, ⎰ storage   o———o Jute ,, ⎰ storage
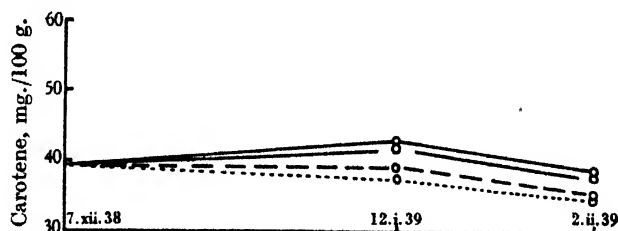
Fig. 3 b. Carotene content of artificially dried grass stored in paper and jute sacks at "summer" and "winter" temperatures estimated by the method of Peterson et al.

o······o Paper sacks ⎱ "Summer"   o———o Paper sacks ⎱ "Winter"
o— — —o Jute ,, ⎰ storage   o———o Jute ,, ⎰ storage

of Ferguson & Bishop (1936), but again no difference could be detected between types of sacks or treatments.

(b) "Winter" versus "summer" storage. Very little difference in the carotene content could be detected between grasses stored either in different containers or at different temperatures, as seen in Table II and Fig. 3 a, b. This finding is surprising, as one would expect a higher rate of destruction of carotene at higher temperatures. It should be remembered, however, that the grass used for this experiment had previously been stored for some time and had already lost 24 % of its original activity. The work of Fraps & Kemmerer (1937), Guilbert (1935) and Russell et al. (1934) has shown that part of the carotene in feeds may be more easily

destroyed while the remainder seems to be much better protected. The above authors have found on the whole greater destruction of carotene in feeds in summer months than in winter, but in several instances given by Fraps & Kemmerer (1937) there was little or no correlation between the carotene lost and the external temperature. Our own results show that temperature is not the only factor governing the destruction of carotene in artificially dried grass.

Whatever the experimental conditions, we were unable to find any difference between jute and paper sacks. This is in agreement with the work of Wilder & Bethke (1938), who state that the type of container, whether paper or jute, had no effect either on the rate or the amount of destruction of carotene in dehydrated alfalfa leaf meal. This work came to our notice after the present experiments were started.

B. The effect of prolonged storage on the carotene and moisture
   content of baled artificially dried grass and of hay

The grasses used for this experiment were obtained by the methods fully described in a previous paper by Bartlett *et al.* (1938). They were stored as pressed bales covered with sacking and kept in the farm food store. The grasses were cut and dried in July 1937 and were sampled again in August 1938; the results are summarized in Table III.

Table III. *Changes in the carotene and moisture content of grass in artificial drying and sun curing and the loss of carotene in the course of* 13 *months' storage*

Method of drying*	July 1937		Aug. 1938		Carotene content as % of that present in fresh grass		Carotene content as % of that present at commencement of storage period
	% moisture	mg. carotene/100 g. grass on dry basis	% moisture	mg. carotene/100 g. grass on dry basis	After drying	After storage	
Fresh grass	88·9	48·9	—	—	—	—	—
Artificially dried:							
High temp.	10·6	43·7	11·6	18·3	89·4	37·4	41·9
Low temp.	12·9	38·2	12 8	13·9	78·1	28·4	36·4
In current of hot air	7·9	42·4	11·4	17·5	86·7	35·8	41·3
Sun dried under natural conditions (hay)	21·4	12·2	13·4	3·9	25·0	8·0	32·0
Dried without sun at air temp.	18·1	15·4	13·9	6·5	31·5	13·3	42·2

* These treatments are fully described in the paper of Bartlett *et al.* (1938).

The moisture of these grasses showed a tendency to reach a level of about 12% regardless of the original value.

With regard to carotene it will be seen that all samples lost a large part of their carotene in the course of a year's storage. Though the absolute amount lost depended on the quantity originally present, the rate of destruction appeared constant and independent of the initial value.

A·loss of 32–42% of carotene during 13 months' storage agrees with that reported by Kane & Shinn (1935), who found losses of 36–40% in alfalfa meals and baled hays after 8 months' storage commencing in March. Camburn et al. (1939) report after 6 months' storage a loss of three-quarters of the carotene content of the original green crop in hays and one-quarter for artificially dried alfalfa meal. Our figures show a loss of 75% of the carotene content during hay-making and 92% during hay-making and 13 months' storage. Artificially dried grass lost 10·6–21·9% of its carotene content on drying and 62·6–71·6% during drying and storage.

PART II. METHODS OF ESTIMATING CAROTENE

The method of Ferguson & Bishop (1936) is chiefly used in this country for estimating carotene and has been regularly used in this laboratory. In the United States of America different methods are used, and we were interested in comparing these various methods. Three representative American methods were tried, namely, the methods of Guilbert (1934), Munsey (1938) and Peterson, Hughes & Freeman (1937), and of these the last one was finally adopted as the most promising and was then systematically compared with the method of Ferguson & Bishop (1936).

These two methods differ in several features. We have summarized in Table IV the essential steps of both procedures, noting their advantages and disadvantages as found in our experience.

A Lovibond Tintometer is used in this laboratory, and the yellow glasses were standardized against the international standard for vitamin A (β-carotene). The same curve was used for both the carotene and the xanthophyll fractions. Moon (1938a) has shown that the error due to the difference in colour intensities of the two pigments is of little consequence, as there is no evidence of the overestimation of the ratio carotene to xanthophyll by the method of Ferguson & Bishop.

At first sight the method of Peterson, Hughes & Freeman (1937) appeared to offer several advantages: (1) At no time is the pigment evaporated to dryness as is the case with the total carotenoid ether

extract in the method of Ferguson & Bishop (1936). (2) No diethyl ether is used and therefore the risk of oxidation of carotene by peroxides is avoided. (3) Readings and calculations are reduced by three-quarters. (4) Small errors in the estimation of the carotene : xanthophyll ratio in the Ferguson & Bishop (1936) method might lead to cumulative errors in the calculation of the carotene content.

Table IV. *Comparison of methods of Ferguson & Bishop (1936) and Peterson, Hughes & Freeman (1937) for the estimation of carotene, as used in this laboratory*

Ferguson & Bishop	Peterson, Hughes & Freeman
1 hr. boiling with aqueous 20% KOH (tendency to froth; needs careful supervision)	½ hr. boiling with 5 g. KOH in 50 ml. of 95% ethyl alcohol (requires occasional shake)
Filter through 17 G3 Jena sintered glass filter,* wash with ether saturated water (this step is very slow for finely powdered meals), then with acetone (residue colourless)	Filter through 17 G3 Jena filter, use ethyl alcohol and petroleum ether to wash residue (filtration very rapid, residue still coloured)
Extract filtrate with peroxide free diethyl ether (carotenoids subjected to danger of oxidation unless the diethyl ether has been recently purified)	Extract filtrate by adding 100 ml. water then re-extract with petroleum ether (B.P. 40–60° C.) (carotene stable in petroleum ether in presence of ethyl alcohol)
Wash four times with 100 ml. water	Wash four times with 100 ml. water (tendency to form awkward emulsions)
Note volume of total carotenoids	
Evaporate an aliquot on water bath,† remove last few ml. of ether on vacuum pump (danger of oxidation)	
Take up in petroleum ether B.P. 60–80° C.	
Phase separation against 92% methyl alcohol	Phase separation against 92% methyl alcohol
Evaluate colorimetrically: (a) total carotenoids, (b) petroleum ether phase "carotene", (c) methyl alcohol phase "xanthophyll"	Evaluate colorimetrically:‡ (a) petroleum ether "carotene" fraction
Calculate carotene : xanthophyll ratio; apply this to total carotenoids to calculate carotene content	

* In the original method a Hirsch funnel with a cotton-wool pad is used.

† Ferguson & Bishop remove ether in a stream of nitrogen on a water bath at a temperature not above 40° C.

‡ As described in the original method, optical density measurements are made spectrophotometrically at wave-lengths 450, 470, 480 mμ.

As a result of estimations carried out at monthly intervals on the artificially dried grass used in the comparison between jute and paper sacks, it was found that the method of Ferguson & Bishop (1936) gave consistently higher results (as seen in Table II) than the method of

Peterson, Hughes & Freeman (1937). In Table V below the result of a test of the statistical significance of mean differences between the two methods shows that the difference is real. The paired t test of "Student" (1908, 1925) was used. The individual values will be found in Table II.

Table V. *Statistical significance of the mean differences between estimations carried out by the methods of Ferguson & Bishop and Peterson, Hughes & Freeman*

Method	Ferguson & Bishop mg. carotene/100 g.	Peterson, Hughes & Freeman mg. carotene/100 g.	Difference	S.E.M.*	P†
Average of 28 estimations	44·02	40·22	+3·8	±0·3564	Greater than 1 : 10,000

* S.E.M. = standard error of the mean.

† P = probability that a mean difference at least as great as the observed mean difference would have arisen by random sampling from a homogeneous population.

In investigating the possible causes of this difference between the two methods we noticed that the residue left on the sintered glass filter after the alcoholic KOH digestion in the method of Peterson, Hughes & Freeman was coloured. It was thought possible that this residue might contain some unextracted carotene. It was therefore washed with ether-saturated water, when a brownish solution was obtained; no colour could be extracted from this by diethyl ether. The residue was further treated with acetone, which removed the remainder of the colour, this was taken up with ether, washed twice with water, evaporated to remove the ether, taken up in petroleum ether and repeatedly shaken with 92% methyl alcohol until no more colour was extracted. About 50% of the extracted colour was retained in the petroleum ether layer. A few tests showed that the additional carotene which can be removed by this further extraction varied from 1 to 4 mg./100 g. depending on the original carotene content of the grass.

Our experience supports Moon's (1939) contention that disadvantages in the use of hot alcoholic KOH are due to the formation of resinous substances from grass which are precipitated in close contact with the carotene and make the subsequent extraction with solvents difficult. This defect is said to be even more pronounced with fine grass meals of the type we were using.

A number of workers, including Wiseman *et al.* (1938), prefer a method of extraction in which the grass is finely ground with glass or sand and the pigments extracted with hot alcohol, followed by treatment of the extract with potash. A few tests carried out in this laboratory showed that for

finely ground artificially dried grass, the extraction is never as complete as when an aqueous KOH digestion is used to break up the plant cells.

Moon (1939) suggests a preliminary breakdown of cellular material with aqueous 20% KOH and then an extraction with industrial spirit followed by petroleum ether. This excludes the possibility of carotene decomposition which might occur in methods using diethyl ether. Our experience speaks certainly in favour of this suggestion.

It should also be borne in mind that the method of Ferguson & Bishop (1936) measures, in addition to the carotene, the xanthophyll fraction; this additional information may be of value, as will be seen in the next part of this paper.

PART III. APPLICATION OF CHROMATOGRAPHIC ANALYSIS TO CAROTENE ESTIMATIONS IN FODDERS

During the progress of the above work interesting information on the carotene : xanthophyll ratios of grasses and hays was obtained. This is set out in Table VI.

It will be seen from Table VI that the carotene : xanthophyll ratio, as estimated by the method of Ferguson & Bishop, was 1 : 2·08 for fresh grass in one case and 1 : 2·21 in another. The ratio increased slightly during drying and quite markedly in sun curing. All these ratios widened on prolonged storage. The highest ratio reached was 1 : 8·24 for a sun cured sample after one year's storage. Similarly (Table VI C) the widening of the carotene : xanthophyll ratio in the process of hay-making was very marked, increasing from 1 : 2·21 for the fresh material to 1 : 4·95 after 96 hr. exposure. The artificially dried grass used in the paper sack experiment had, as will be seen from Table VI B, an initial ratio 1 : 1·23; after 6 months' storage the value was unchanged at 1 : 1·27.

These findings are in agreement with the work of Moon (1938a), who reported ratios of 1 : 2·23–1 : 2·50 as average values for fresh grass and artificially dried grass, the latter, however, was subject to considerable variations, ranging from 1 : 1·11 to 1 : 10·00. The ratios for hays were higher than for artificially dried grass.

In Table VI the carotene and xanthophyll values for the grasses studied are set out, and they show a relatively greater loss of carotene than of xanthophyll during storage or curing. The loss for group A grasses during 13 months' storage was from 52·5 to 70·5% for carotene and from 34·8 to 56·0 for xanthophyll.

In group C the loss during 96 hr. hay-making was 80·2% for carotene and 55·3% for xanthophyll.

Table VI. *Changes in the carotene and xanthophyll content of grasses and in the carotene : xanthophyll ratio during artificial drying and hay-making and during storage*

Description of grass	Carotene* mg./100 g.			Xanthophyll* mg./100 g.			Ratio	
	1937	1938	% loss on storage	1937	1938	% loss on storage	1937	1938
Fresh	39·8	—	—	82·7	—	—	1 : 2·08	—
A. (a) Artificially dried, high temp.	38·3	18·2	52·5	83·3	54·3	34·8	1 : 2·18	1 : 2·99
(b) Artificially dried, low temp.	28·1	12·0	57·2	68·9	40·5	41·2	1 : 2·45	1 : 3·37
(c) Artificially dried, current hot air	32·5	14·3	56·1	77·8	51·4	34·0	1 : 2·24	1 : 3·59
(d) Sun dried	12·1	4·1	70·5	56·9	33·8	40·0	1 : 4·64	1 : 8·24
(e) Dried at atmospheric temperature without sun	15·5	5·7	63·0	64·1	29·8	56·0	1 : 4·14	1 : 5·22
	Aug. 1938	Feb. 1939		Aug. 1938	Feb. 1939		Aug. 1938	Feb. 1939
B. Artificially dried grass, paper sack experiment	54·7	34·9	36·2	67·5	44·3	34·3	1 : 1·23	1 : 1·27

Destruction of carotene and xanthophyll in the sun curing of grasses

	Hours after cutting	Caroteno* mg./100 g.	Xanthophyll* mg./100 g.	Ratio
C.†	Fresh	22·4	49·4	1 : 2·21
	1	18·5	44·4	1 : 2·39
	3	16·6	40·4	1 : 2·43
	6	13·6	36·6	1 : 2·67
	24	11·7	30·9	1 : 2·64
	48	12·3	35·0	1 : 2·83
	72	5·3	28·0	1 : 5·33
	96	4·4	22·1	1 : 4·95
	% loss on curing	80·2	55·3	

* The carotene and xanthophyll values are given as calculated directly from the petroleum ether and methyl alcohol phases, without the application of the carotene : xanthophyll ratio to the total carotenoids.

† For further details see paper by Bartlett *et al.* (1938), Table V.

Moon (1938*a*, 1938*b*) reported greater loss of carotene than of xanthophyll in low temperature (55° C.) drying and in hay-making.

Virtanen (1933), Peterson *et al.* (1935), Peterson, Bird & Beeson (1937), and Hayden *et al.* (1937) all found abnormally high values for the carotene in A.I.V. silage, in some cases higher than for carotene in the original forage. Kane *et al.* (1936) found that pigments other than carotene were present in the "carotene fractions" from A.I.V. silage. Quackenbush *et al.* (1938) found three pigments other than carotene in the petroleum ether fractions of A.I.V. silage. These were separated from carotene by chromatograms using magnesium oxide and were found to

be biologically inactive. At times 40% of the colour of the carotene fraction was due to these impurities. They also showed that pigments soluble in petroleum ether were formed by the action of acids on lutein. On the other hand, Taylor *et al.* (1939), who carried out biological and colorimetric estimations of carotene in silage, stated that the formation of new carotenoids by the action of acid on green plant tissues did not interfere with the accuracy of the colorimetric carotene determination as a measure of vitamin A potency.

It appeared therefore possible that the widening of the carotene : xanthophyll ratio in dried grass and hay is not simply an expression of the relative stability of carotene and xanthophyll but that the formation of decomposition products of both, soluble in either petroleum ether or in methyl alcohol might complicate the picture. For this reason we thought it advisable to carry out chromatographic analyses on the petroleum ether ("carotene") fractions obtained from the artificially dried grass used in the paper and jute sack storage experiment.

A preliminary investigation in December 1938 showed the presence of a pigment other than carotene in the petroleum ether phase.

Subsequently the work of Wiseman *et al.* (1938) came to our notice. They showed that coloured impurities present in the carotene fractions from hays and silage account for about 32% of the absorption of the carotene extract at wave-length 450 mμ.

Further work was started by us in February 1939. Petroleum ether extracts prepared by the methods of Ferguson & Bishop (1936) and Peterson, Hughes & Freeman (1937) were passed through test-tube towers of aluminium oxide (Merck after Brockman) mixed with diluent alumina in the ratio of 1 : 1. The petroleum ether fractions were washed four times with water prior to adsorption to remove all traces of alcohol, and were then dried over anhydrous sodium sulphate, cooled in a refrigerator and passed ice-cold through the tower. The strength of the solution was measured colorimetrically just prior to chilling. During adsorption two distinct bands were developed, the lower pink band was β-carotene; above it, separated by a clear portion, another yellow pigment was deposited at the top of the column. At times, a faint band of pseudo-α-carotene (Gillam & El Ridi, 1936) was obtained below the β-carotene band. When the chromatogram was fully developed, the two main bands were cut out and taken up separately in petroleum ether and their colour intensities measured, assuming both to be carotene. The combined values were always lower than the original readings taken before adsorption, the loss was about 12%, ranging from 8·9 to 20·4%. Willstaedt & With

(1938) reported losses up to 48% on adsorption on aluminium oxide. For this reason Hegsted et al. (1939) used calcium carbonate rather than magnesium oxide or aluminium oxide.

We found that cooling prior to adsorption reduced the loss, but that it was not altered by working in darkness. Adsorption on $CaCO_3$ showed that the unknown pigment (pigment x), like carotene, passed down the column in front of lutein. The results of chromatographic analysis are set out in Table VII. Approximately 2 g. portions of grass were used.

Table VII. *Results of chromatographic analysis of "carotene" fractions*

Sample mg./100 g.	A					B	C	D
Total "carotene" before adsorption	35·6 (F.B.)	31·2 (P.)	31·3 (P.)	31·0 (P.)	30·4 (P.)	31·6	6·3 (P.)	1·78 (F.B.)
Pigment x	8·7	9·2	8·2	8·2	7·9	6·5	0·8	0·05
β – carotene	21·1	18·0	18·4	19·4	19·8	21·2	3·9	1·66
Total recovered after adsorption	29·8	27·2	26·6	27·6	27·7	27·7	4·7	1·71
Pigment x expressed as % of total recovered	29·3	33·8	30·8	29·7	28·5	23·5	20·5	3·0

Samples A and B. Artificially dried grass meal stored 6 months, repeats from one sample.

A. Analysed by methods of Peterson, Hughes & Freeman (P.) and Ferguson & Bishop (F.B.).

B. A petroleum ether extract prepared from the same batch of artificially dried grass by the cold extraction method of Wiseman et al. (1938).

C. A sample of dried grass stored in bales 18 months and low in carotene analysed by the method of Peterson, Hughes & Freeman (1937).

D. A petroleum ether extract of fresh grass (13 April 1939) cut from a lawn into a dark tin and analysed immediately by the method of Ferguson & Bishop (1936).

A trial sample of a grass silage prepared by a heat process gave results essentially similar to those with artificially dried grass. It will be seen in Table VII that although pigment x amounted to 20·5–33·8% of the total pigments recovered in dried grass, it was present only in small amounts in quickly grown early spring grass. The results obtained with the cold extraction method show, on the other hand, that the pigment is not a heat artefact produced in the course of the usual extraction. According to Munsey (1939) the impurities in the "carotene" fraction may amount to 30% depending on the type of material, being greater in low grade hays than in fresh grasses.

A petroleum ether solution of pigment x prepared by chromatographic analysis was sent to Dr Gillam of Manchester University who kindly supplied the data set out in Table VIII.

An attempt was made to separate pigment x from β-carotene by using various concentrations of methyl alcohol in the phase separation;

however, this proved impossible, the solubility of the two pigments being very similar.

By the use of a solution of diacetone alcohol in water instead of 92 % methyl alcohol Hegsted *et al.* (1939) were able to get a more accurate measure of the β-carotene content of silage.

Table VIII. *Absorption spectrum of pigment x in different solvents.*
Absorption maxima in visible light

C_2H_5OH	472 and 444 mμ.	CS_2	501 and 471 mμ.
Petroleum ether, B.P. 60–80° C.	473 and 444 mμ.	$CHCl_3$	482 and 452 mμ.

Antimony trichloride gave a slate blue colour showing end absorption in the red beyond 630 mμ and apparently no other selective absorption.

Fraps & Kemmerer (1939) attempted to overcome the difficulty by a modified adsorption technique; the crude carotene solution was shaken with a selective magnesium hydroxide, which left only carotene in solution.

Biological tests on rats showed that pigment x is devoid of vitamin A activity. Chromatographic analysis or the use of special solvents are therefore necessary for the accurate determination of the pro-vitamin A (carotene) content of dried grass and hay.

SUMMARY

1. The influence of storage in the light and in the dark at ordinary temperature and in a heated room at 70–80° F. on the carotene content of finely ground artificially dried grass stored in paper sacks and jute sacks was studied. There was an initial drop in carotene content from 61·1 to 46·5 mg./100 g., i.e. 23·9 %, in the first month, and a total loss of 31·4 % during 6 months' storage (August to February). No difference could be detected either between treatments or types of containers.

2. There was a marked loss of carotene during 13 months' storage of baled artificially dried grass and of hays, amounting to 30–40 % of the original value.

3. Two methods of estimating carotene were compared. The method of Ferguson & Bishop (1936) gave higher results than the method of Peterson, Hughes & Freeman (1937). The difference is probably due to incomplete extraction in the latter method.

4. Chromatographic analyses of "carotene" fractions from the above grasses showed the presence of coloured impurities amounting to 20·5–33·8 % of the total recovered pigments.

5. As these impurities are biologically inactive, chromatographic analysis or the use of special solvents are probably necessary for the accurate determination of carotene in forage.

REFERENCES

BARTLETT, S., HENRY, K. M., KON, S. K., OSBORNE, L. W., THOMPSON, S. Y. & TINSLEY, J. (1938). *Biochem. J.* 32, 2024.

CAMBURN, D. M., ELLENBERGER, H. B. & CROOKS, G. C. (1939). *J. Dairy Sci.* 22, 456.

FERGUSON, W. S. & BISHOP, G. (1936). *Analyst*, 61, 515.

FRAPS, G. S. & KEMMERER, A. R. (1937). *Bull. Tex. agric. Exp. Sta.* no. 557.

—— —— (1939). *J. Ass. off. agric. Chem.* 22, 190.

GILLAM, A. E. & EL RIDI, M. S. (1936). *Biochem. J.* 30, 1735.

GUILBERT, H. R. (1934). *Industr. Engng Chem.* (Anal. ed.), 6, 452.

—— (1935). *J. Nutrit.* 10, 45.

HAYDEN, C. C., PERKINS, A. E., KRAUSS, W. E., MONROE, C. F. & WASHBURN, R. G. (1937). *Bi-m. Bull. Ohio agric. Exp. Sta.* 22, 21.

HEGSTED, D. M., PORTER, J. W. & PETERSON, W. H. (1939). *Industr. Engng Chem.* (Anal. ed.), 11, 256.

KANE, E. A. & SHINN, L. A. (1935). *J. biol. Chem.* 109, xlviii.

KANE, E. A., WISEMAN, H. G., HARTMAN, A. H. & CARY, C. A. (1936). *J. Dairy Sci.* 19, 466.

MOON, F. E. (1938 a). *J. Soc. chem. Ind.* 57, 457.

—— (1938 b). *J. Soc. chem. Ind.* 57, 455.

—— (1939). *J. agric. Sci.* 29, 295.

MUNSEY, V. E. (1938). *J. Ass. off. agric. Chem.* 21, 331.

—— (1939). *J. Ass. off. agric. Chem.* 22, 664.

PETERSON, W. H., BIRD, H. R. & BEESON, W. M. (1937). *J. Dairy Sci.* 20, 611.

PETERSON, W. H., BOHSTEDT, G., BIRD, H. R. & BEESON, W. M. (1935). *J. Dairy Sci.* 18, 63.

PETERSON, W. H., HUGHES, J. S. & FREEMAN, H. F. (1937). *Industr. Engng Chem.* (Anal. ed.), 9, 71.

QUACKENBUSH, F. W., STEENBOCK, H. & PETERSON, W. H. (1938). *J. Amer. chem. Soc.* **60**, 2937.

RUSSELL, W. C., TAYLOR, M. W. & CHICHESTER, D. F. (1934). *Bull. N.J. agric. Exp. Sta.* no. 560.

"STUDENT" (1908). *Biometrika*, **6**, 1.

—— (1925). *Metron*, **5**, 105.

TAYLOR, M. W., RUSSELL, W. C. & BENDER, C. B. (1939). *J. Dairy Sci.* **22**, 591.

VIRTANEN, A. I. (1933). *Biochem. Z.* **258**, 251.

WILDER, O. H. M. & BETHKE, R. M. (1938). *Bull. Ohio agric. Exp. Sta.* no. 592.

WILLSTAEDT, H. & WITH, T. K. (1938). *Hoppe-Seyl. Z.* **253**, 40.

WISEMAN, H. G., KANE, E. A., SHINN, L. A. & CARY, C. A. (1938). *J. agric. Res.* **57**, 635.

THE MINERALS IN THE CLAY FRACTIONS OF A BLACK COTTON SOIL AND A RED EARTH FROM HYDERABAD, DECCAN STATE, INDIA

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(With Plate XII and Two Text-figures)

METHODS for determining the mineral constituents of soil colloids have recently been discussed by Nagelschmidt (1939). These methods were applied to soil samples from a typical black cotton soil (or Regur) and a typical red earth from Hyderabad, Deccan State, India, which have been studied in detail by Desai (1939).

The two soil profiles selected for this study were taken on and near the Government Experimental Farm, Rudrur, Nizamabad. The climate of the district is characterized by cool, dry winters, a rainy season which extends from June to October and a summer season, February to June, during which severe local storms may occur. The total rainfall ranges between 37 and 40 in. per annum.

The black cotton soil (no. P7 in Desai, 1939) was taken from an irrigated area on the farm. It was derived from colluvium over gneiss and consisted of a dark greyish heavy clay loam which was hard and compact to the lowest depth of sampling, 48 in. The fine material contained little calcium carbonate, but some nodules and concretions were distributed throughout the profile; there was no pronounced zone of carbonate accumulation. Its pH values increased with depth from 8·0 to 8·4, and the soluble salt content varied between 0·05 and 0·07 %.

The red earth (no. P8 in Desai, 1939) was taken on uncultivated waste land on the slope of a granite hill near the farm. It was a brownish red coarse sandy clay loam, becoming lighter in colour with depth, and containing disintegrating rock material in the lowest sample, 36–42 in. The pH values increased with depth from 6·1 to 7·4, no carbonates being

present. The soluble salts varied between 0·04 and 0·06%, except for one high value 0·09% at 6–18 in.

MECHANICAL ANALYSIS

The samples of the black cotton soil contained about 5% stones, larger than 2 mm. These were mainly greyish carbonate nodules with a few rock fragments of weathered granite similar to those found in the red soil, and some pieces of vein quartz. The soils of the red earth, P8, had far more (30–40%) stones consisting entirely of weathered fragments of coarsely crystalline granite or gneiss.

Mechanical analyses for six samples of each profile are given in Table I. The data show that there is very little variation within each profile. The black soil has 60–70% silt and clay, whereas the red soil has only 25–40%.

Table I. *Mechanical analyses: oven-dry fractions as percentage of oven-dry soil below 2 mm.*

Depth in.	Coarse sand	Fine sand	Silt	Clay	Air-dry moisture
Black cotton soil (P7)					
0–6	23·0	13·2	22·6	39·9	6·6
6–12	21·8	14·0	22·8	41·1	6·6
12–18	23·2	13·7	23·6	39·7	6·2
18–24	22·2	12·6	22·8	41·7	6·6
30–36	21·4	12·4	23·2	43·3	6·8
42–48	20·1	11·9	23·1	44·7	6·9
Red earth (P8)					
0–6	52·2	23·0	5·9	20·0	2·5
6–18	46·4	15·9	6·5	31·8	4·2
18–24	48·8	13·5	7·8	32·0	4·4
24–30	51·7	15·0	7·9	26·8	3·8
30–36	48·0	15·3	9·0	29·0	4·1
36–42	47·0	13·8	8·7	31·3	4·5

Clay fractions were prepared by treating the soils with hydrogen peroxide and acetic acid, washing till the filtrates were free from calcium, and dispersing with ammonia. The clay was separated by repeated decantations at 8·5 cm. after 24 hr.

The clay suspension was subdivided into three fractions, coarse, fine and superfine clay, by repeated supercentrifuging at 23,000 rev./min. with rates of flow of 120 l./hr. and 12 l./hr. The estimated particle sizes of the three fractions were:

Coarse clay	1·4–0·1 μ diameter
Fine clay	0·1–0·06 μ diameter
Superfine clay	Under 0·06 μ diameter

Quantitative results for two representative samples of each profile are shown in Table II. In both profiles the coarse clay forms the smallest and the superfine clay the largest fraction. The proportions of coarse, fine and superfine clay are constant throughout the black profile, but for the red profile the superfine clay increases with depth at the expense of the fine one.

Table II. *Clay subfractions as percentages of total clay*

Soil	Depth in.	Coarse clay	Fine clay	Superfine clay
Black	12–18	10	25	65
Black	42–48	11	22	67
Red	18–24	7·5	43·5	49
Red	36–42	8·5	27·5	64

CHEMICAL ANALYSIS OF CLAY SUBFRACTIONS

Silicate analyses were carried out on all fractions obtained from the two soil profiles. The results show that in each case there is very little variation with increasing depth. As the full data are being published elsewhere (Desai, 1939), it seems sufficient to give results only for one layer from each profile. The data are shown in Table III and include the base exchange capacities determined by the Parker (1929) method, silica-alumina and silica-sesquioxide ratios and the organic carbon determined by the modified chromic acid method (Robertson & Shewan, 1935).

Table III. *Chemical analyses of clay subfractions for one black cotton soil* (P7) *and one red earth* (P8), *as percentages of oven-dry clays*

	Black soil, 12–18 in.			Red earth, 18–24 in.		
	Coarse %	Fine %	Superfine %	Coarse %	Fine %	Superfine %
SiO_2	57·30	47·70	49·40	46·39	42·07	45·43
Al_2O_3	16·00	23·00	22·80	25·04	26·01	26·37
Fe_2O_3	10·60	11·90	12·00	11·79	15·48	10·91
TiO_2	2·00	1·39	0·30	1·54	0·94	0·22
MnO	0·05	0·05	0·04	0·05	0·05	0·04
CaO	0·58	0·22	Nil	0·49	0·48	0·53
MgO	2·38	2·30	1·95	1·08	1·03	1·02
Na_2O	0·77	0·39	0·28	0·55	0·55	0·28
K_2O	1·71	1·35	0·71	2·13	1·00	0·67
P_2O_5	0·10	0·14	0·11	0·17	0·24	0·21
Ignition loss	9·04	12·30	13·70	10·93	13·09	14·68
Total	100·53	100·74	101·29	100·16	100·94	100·36
SiO_2/Al_2O_3	6·1	3·5	3·7	3·2	2·8	2·9
SiO_2/R_2O_3	4·3	2·7	2·8	2·4	2·0	2·3
Exchange capacity in mg. equivalent per 100 g. clay	34	75	99	23	36	49
Organic carbon	—	2·08	2·44	—	1·65	1·70

DETERMINATION OF FREE OXIDES

Free silica, alumina and iron oxide were determined by the hydrogen sulphide method of Drosdoff & Truog (1935). The amounts dissolved and the base exchange capacity before and after the treatment were determined on one unfractionated clay sample of each profile and on one fine and superfine clay sample of the red earth. The results are shown in Table IV. A number of samples were subjected to the modified Truog treatment using sodium sulphide and oxalic acid (Truog *et al.* 1937). This method is more drastic and the total loss of material is higher, 40% of the superfine red fraction being dissolved as against 10% with hydrogen sulphide. It is likely that in this process the silicates present are attacked to some extent (cp. Raychaudhuri, 1936; Toth, 1939).

Table IV. *Alumina, iron oxide and silica, as percentage of clay, dissolved by treatment with hydrogen sulphide according to Drosdoff & Truog (1935), and base exchange capacities in mg. equiv. per 100 g. clay before and after the treatment*

	Black whole clay 42–48 in.	Red whole clay 24–30 in.	Red fine clay 24–30 in.	Red superfine clay 24–30 in.
SiO_2	2·30	3·98	2·37	2·62
Al_2O_3	0·56	1·10	0·57	1·29
Fe_2O_3	4·85	6·98	13·40	5·70
Base exchange capacity:				
Before treatment	83	35	—	—
After treatment	58	30	—	—

DEHYDRATION DATA

Dehydration curves were taken for three depths in each profile by the method of intermittent heating. Again, there was little or no variation with depth for each profile. Characteristic curves are shown in Text-fig. 1. The water lost at 105° increased rapidly with decreasing grain size for all fractions, and was consistently about 1% higher for fractions from black soils than for the corresponding red ones. The pronounced difference in the form of the curves for red and black soils, especially between 400 and 600°, is discussed in detail later (pp. 647, 650).

X-RAY DATA

Powder and aggregate diagrams were taken for most of the samples and it was found that throughout each profile the clay fractions of equal grain size gave identical diagrams. There were, however, differences between the diagrams from the two profiles and also between the coarse,
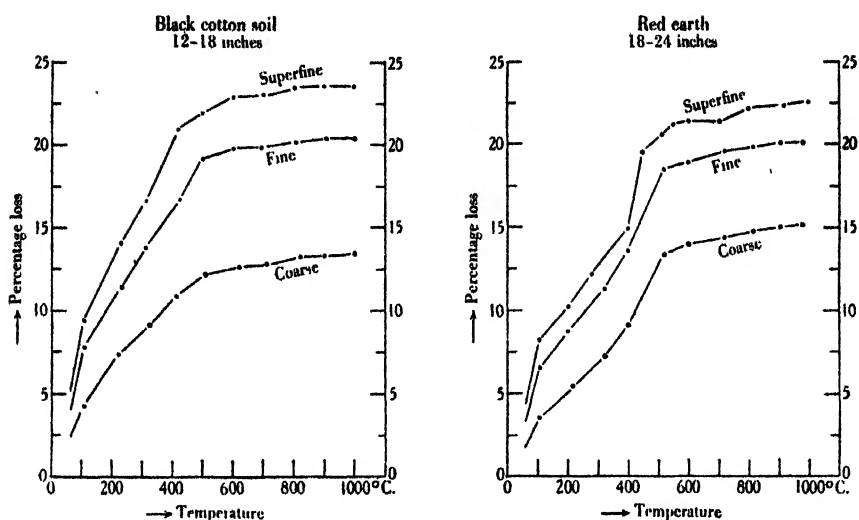
Text-fig. 1. Dehydration curves of clay subfractions from black cotton soil and red earth, by the method of intermittent heating. Loss in weight as percentage of air-dry fractions.
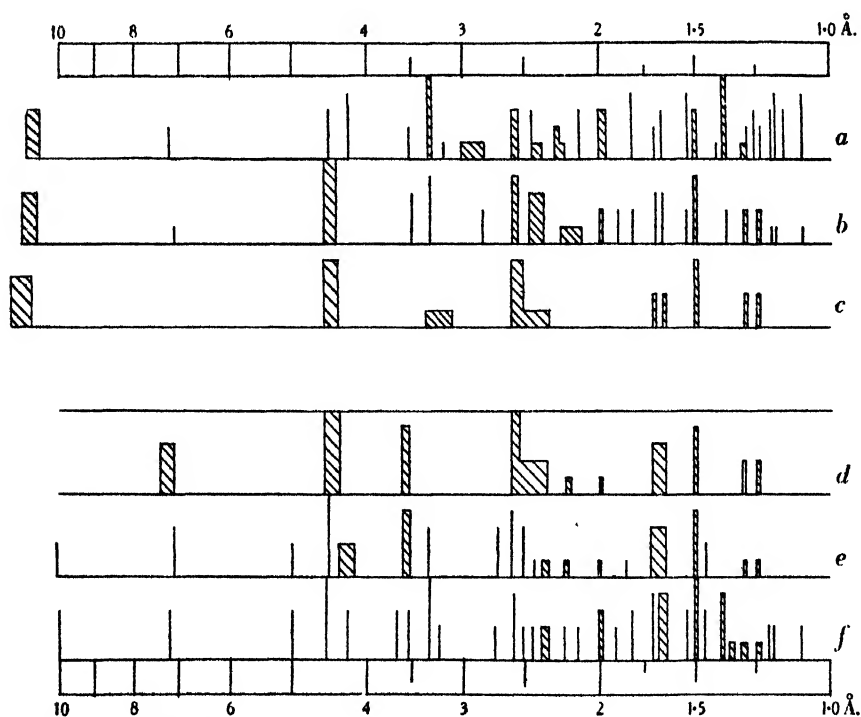
Text-fig. 2. X-ray data for black cotton soil (a) coarse, (b) fine, (c) superfine clay and red earth, (d) superfine, (e) fine, (f) coarse clay.

fine and superfine fractions of any one clay. This confirms the chemical data and shows that there is no noticeable variation in the mineralogical composition throughout each profile.

Text-fig. 2 shows the diffraction data in the form described previously (Nagelschmidt, 1939), and Pl. XII shows some of the diagrams. Diagrams were also taken for samples after treatment by the sodium sulphide-oxalic acid method (Truog *et al.* 1937). For all black clays there was no difference between treated and untreated samples, but for most of the red clay samples the diagrams of the treated material contained fewer lines, and, except for one line, the difference could be explained as due to the disappearance of hematite, $\alpha\text{-Fe}_2\text{O}_3$. The one line not due to hematite coincided with one of the strong lines of goethite, $\alpha\text{-FeOOH}$, which may have been present in very small amounts. There was no indication of the presence of crystalline aluminium hydroxides.

Diagrams of samples of the black clay at different moisture contents showed the lattice shrinkage and expansion characteristic of a member of the montmorillonite group. The red clays failed to show this effect under the same conditions. Aggregate diagrams of the air-dry black clay showed the basal spacing to be about 12 A.; the corresponding diffraction line was blurred and not very strong. By the method of separation the exchangeable ions of this clay were ammonium and hydrogen, but after the material had been leached with calcium chloride and the excess chloride washed out, new air-dry aggregates showed a stronger basal spacing of 15 A. The replacement of ammonium and hydrogen by calcium would explain this change in the basal spacing at constant relative humidity. Similar results for supercentrifuged bentonite fractions have been reported previously (Nagelschmidt, 1939). The basal reflexions of the soil colloids were, however, less intense than those of the bentonite. The interpretation of the X-ray diagrams is given in Table V.

Table V. *Minerals identified by X-ray diffraction in clay subfractions*

	Black cotton soil, 12–18 in.			Red earth, 18–24 in.		
	Coarse	Fine	Superfine	Coarse	Fine	Superfine
Quartz	Much	Little	Nil	Medium	Trace	Nil
Mica	Trace	Trace	Nil	Little	Little	Nil
Kaolinite or halloysite	Little	Little	Nil	Much	Much	Much
Montmorillonite or beidellite	Medium	Much	Much	Nil	Nil	Little?
Hematite and goethite	Nil	Nil	Nil	Little	Little	Trace

Optical data

A petrological examination of the sand fractions from one sample of each profile was carried out by Dr R. Hart, to whom our thanks are due for the following information. "The black soil contained mainly quartz and a few grains of felspar, hornblende and some iron oxide, while the red soil contained the same minerals and, in addition, some brown mica. There was much more felspar and ferromagnesian minerals in the red soil than in the black one, and the quartz was much more heavily stained by iron oxides."

The refractive indices of some of the superfine clay samples were measured in sodium light with a mixture of olive oil, cinnamon oil and bromo naphthalene, as recommended by Correns & Mehmel (1936). The samples were saturated with calcium and measured after they had reached equilibrium weight, at room temperature at 50% relative humidity, and again after drying at 105° C., both before and after sodium sulphide-oxalic acid treatment (Truog et al. 1937). The results for $n\gamma$ are given in Table VI. The double refraction of the black samples of the order of 0·013 was not noticeably affected by the drying or by the Truog treatment, and the double refraction of the red samples was not affected by the drying; it was, however, reduced by the Truog treatment from 0·017 to 0·010.

Table VI. *Refractive index $n\gamma$ determined in sodium light for superfine clay fractions before and after Truog treatment and at two temperatures*

| | Black cotton soil, 12–18 in. | | Red earth, 18–24 in. | |
Drying	Superfine	Truog-treated superfine	Superfine	Truog-treated superfine
50% R.H.	1·579	1·577	1·588	1·581
Oven-dry	1·592	1·588	1·600	1·585

Correlation of results

Although a general knowledge of the minerals present in a soil colloid can be obtained by adequate X-ray diffraction data alone, this knowledge is made more certain and can be refined by using chemical, dehydration and optical data. In this way quantitative statements can be made and the fitting together of the various observations checked. We shall first consider the clay of the black cotton soil (12–18 in.) and then that of the red earth (18–24 in.), in both cases beginning with the superfine fractions.

BLACK CLAY SUPERFINE FRACTION

This fraction shows from the X-ray data only one crystallized mineral, a member of the montmorillonite group. The observed base exchange capacity of 99 mg. equivalent per 100 g. clay is in good agreement with this observation. Its composition (Table III) closely resembles that of beidellite from Beidell, Saguache Co., Colorado (Larsen & Wherry, 1917), as can be seen by comparing the percentages for silica, alumina and iron oxide for beidellite and the superfine fraction, calculated in both cases for ignited material.

	Beidellite from Beidell %	Black superfine clay %
SiO_2	58·6	57·7
Al_2O_3	25·1	26·6
Fe_2O_3	10·8	14·0

In order to see whether appreciable amounts of amorphous material were present in the soil colloid, hydrogen sulphide treatments (Drosdoff & Truog, 1935) were given to the superfine black clay and also to the beidellite from Beidell. The amounts of silica, iron oxide and alumina dissolved were as percentages of the air-dry material.

	Beidellite from Beidell %	Black superfine clay %
SiO_2	3·59	3·02
Al_2O_3	0·23	0·14
Fe_2O_3	5·64	4·06

Both materials were slightly attacked by this treatment, but there was no evidence for the presence of large amounts of amorphous material in the superfine black clay.

A method of calculating isomorphous replacements and base exchange capacities for members of the montmorillonite group has been described by Nagelschmidt (1938). By this method the superfine black clay contains in the silicon layer $Si_{3·49}$ $Al_{0·51}$ instead of Si_4 and in the aluminium layer $Al_{1·38}$ $Fe_{0·62}$, no divalent ions being present, instead of Al_2. The calculated base exchange capacity is 120 mg. equivalent per 100 g. oven-dry material which is somewhat in excess of the observed value of 99 mg. equivalent per 100 g.

Grim (1939) has recently suggested that the mica type material (illite) has negative charges due to isomorphous replacements mainly in the silicon layers, whereas the montmorillonite type with variable basal

spacing has these replacements mainly in the aluminium layer. The observations on the black superfine colloid do not seem to bear this out, as there is a variable basal spacing and the replacements are mainly in the silicon layers. It can be argued, however, that the iron oxide determined may include an unknown amount of divalent iron.

The dehydration curve of the superfine black clay differs from known montmorillonite or bentonite dehydration curves in being almost straight up to about 500°, whereas in montmorillonite little water is lost between 300 and 450°. Unfortunately, through lack of material, we were unable to take a dehydration curve of beidellite. It is possible that the iron in beidellite causes its dehydration curve to be different from that for montmorillonite.

The refractive index of the superfine black clay at 105°, $n\gamma = 1.592$, is very similar to the refractive index of beidellite from Beidell, taken at 105°, $n\gamma = 1.589$, but the air-dry values are somewhat different. This deviation may be due to differences in water content and exchangeable ions.

Black clay fine fraction

This fraction contains, according to the X-ray data, much montmorillonite, little quartz and kaolinite and very little mica. The estimation of kaolinite and mica is mainly based on the intensities of basal reflexions on aggregate diagrams, the estimation of quartz on reflexions at larger angles of diffraction.

In order to determine the amount of kaolinite present the dehydration curve is usually of great help, as kaolinite loses more than 10% of water between 350 and 500°, whereas montmorillonite or mica lose only 2–3% in this interval. The curve of the superfine black clay is, however, different from montmorillonite curves; it is, therefore, impossible to estimate the kaolinite from these curves. It seems, however, permissible to assume as a first approximation that the base exchange capacity and chemical composition of the Beidellite, which was identified as the only constituent of the superfine fraction, are constant from superfine to coarse clay. With this assumption 75% of beidellite would be a maximum estimate for the fine fraction if the other minerals present had no base exchange capacity at all. Actually the base exchange capacity of kaolinite is low, and could hardly account for more than 10 mg. equivalent %, and mica is only present in very small amounts. 60% of beidellite would therefore seem a minimum and 70% the most likely value. If we now subtract the equivalent of 70% of the superfine fraction from the fine fraction, using

the chemical data in Table III, we are left with a residue of $13\cdot1\%$ SiO_2 and $7\cdot1\%$ Al_2O_3, both as percentage of the fine fraction. The aluminium is mainly present in kaolinite and a small proportion in mica. It is therefore possible to state that 17% kaolinite and 5% quartz are maximum estimates under the above assumptions. Actually both percentages should be somewhat smaller, as there is some mica present.

The mica in soil colloids may vary widely in chemical composition, but in comparable materials the potassium content is probably the best guide. The lowest potassium content recorded by Grim *et al.* (1937) for illite is $4\cdot7\%$ K_2O, but earlier data by Denison *et al.* (1929) seem to indicate that much lower amounts, down to less than 1%, can occur in coarse mica in soils. The K_2O content of the fine black clay is $0\cdot64\%$ larger than the K_2O content of the superfine fraction. On the basis of 5% K_2O for the mica in soil colloids in general this would correspond to 13% of mica in the fine fraction. As it seems impossible to isolate the mica from the black clay, there is no proof that this figure is correct, but higher values seem very unlikely from the X-ray data, especially from the intensity of the basal 10 A. reflexion. Recently, Hendricks & Alexander (1939) have suggested that minerals with mixed structures between hydromica and montmorillonite may frequently occur in soil colloids, and although no details about such minerals are known, it seems likely that their basal reflexions would be blurred and weaker than those of the pure minerals; in this way estimates based on X-ray data alone would tend to be too low in comparison with estimates for layer-lattice minerals such as kaolinite, which do not form such mixed structures. For the various reasons given above, it is not possible to determine the various constituents with great accuracy, but the following are the extreme amounts which may be present: beidellite $60-75\%$, kaolinite $5-20\%$, mica $5-20\%$, quartz $2-10\%$. The most likely composition is beidellite 70%, kaolinite 10%, mica 15%, quartz 5%.

BLACK CLAY COARSE FRACTION ·

This fraction contains according to the X-ray data much quartz, medium beidellite, little kaolinite and a trace of mica. If the considerations elaborated above for the fine fraction are applied, it is seen that the limiting values for the different constituents are: quartz $25-32\%$, beidellite $25-35\%$, kaolinite $10-23\%$, mica $5-25\%$. The most likely values are: beidellite 30%, quartz 30%, kaolinite 15%, mica 15%. The analytical data also show that there is too much iron present to be

accommodated in beidellite and mica on the assumption that the beidellite has the composition of the superfine fraction. It seems that 4% Fe_2O_3 is present as amorphous or crystalline hydroxide or oxide. As amounts less than 5% of goethite in mixtures with other soil colloid minerals can probably not be detected by X-ray diagrams, this result is consistent with the X-ray data.

The total water content of the coarse fraction is 66% of the water content of the superfine fraction, and if we take all minerals other than quartz together as being hydrated, we get a rough estimate for quartz of 34%, which does not deviate much from the composite estimate of 30% given above.

Red clay superfine fraction

According to the X-ray data, this fraction contains much kaolinite or halloysite, and only a trace of iron oxide or hydroxide. If we assume that all aluminium shown in the analysis of this fraction in Table III represents a kaolinite of theoretical composition, we get a value of 67% kaolinite and are left with a residue of 14·5% SiO_2 and 10·9% Fe_2O_3. The SiO_2 cannot be quartz, as such amounts of quartz would show up on the X-ray diagrams, but it also cannot be amorphous silica, as the Truog treatment dissolves less than 3% of SiO_2, and amorphous silica should be dissolved by that treatment. The presence of a hypothetical iron kaolinite, which would account for the excess silica, seems very unlikely, although it cannot at the present stage of our knowledge be definitely ruled out for soil colloids. It was decided, therefore, to use a sodium sulphide-oxalic acid treatment to remove iron oxides, followed by prolonged heating at 510° to destroy kaolinite. This treatment should destroy all crystalline materials recognized in the original X-ray data. The X-ray diagrams of the treated material showed a number of weak lines corresponding to hkO reflexions of montmorillonite or beidellite, but no lines corresponding to their basal reflexions. Aggregate diagrams of the heated material showed no clear basal reflexions.

Aggregates of the calcium-saturated original air-dry superfine fraction showed, besides strong kaolinite basal reflexions, only a doubtful trace of a 15 A. line. The presence of beidellite in this fraction is therefore possible but not quite certain. It would account for part of the base exchange capacity of 49 mg. equivalent per 100 g. clay, which is higher than would be expected for kaolinite, and for part of the loss of water below 300° C., which is also higher than would be expected for kaolinite or halloysite

in the presence of less than 3% organic matter. The properties of this fraction seem to correspond closely to the data given by Kelley *et al.* (1939) for the Vina colloids.

The dehydration curve of this fraction shows that the bulk of the lattice hydroxyl of the kaolinite is given up below 450° C., which would, according to the dehydration curves of Ross & Kerr (1934), indicate halloysite rather than kaolinite, but it has been shown previously (Nagelschmidt, 1939) that these two minerals cannot be distinguished in soil colloids. The refractive index, even after the sodium sulphide-oxalic acid treatment (Truog *et al.* 1937) is higher than would be expected for kaolinite.

On summarizing our evidence it can only be said that about 60% of the fraction consists of kaolinite or halloysite and less than 10% of iron oxide and hydroxide. Up to 30% of it may be due to a member of the montmorillonite group.

<center>RED CLAY FINE FRACTION</center>

According to the X-ray data, this fraction also contains much kaolinite or halloysite, and in addition a little hematite, mica and a trace of quartz. From the chemical and dehydration data kaolinite forms 50–60% of the fraction. The amount of Fe_2O_3 dissolved by the hydrogen-sulphide treatment (Drosdoff & Truog, 1935) is 10%, which gives an upper limit for free iron oxide, the remaining iron being partly in the mica and partly perhaps in a member of the montmorillonite group. The quartz content is less than 5%, this estimate being based on the X-ray diffraction data. It again seems that there is slightly more SiO_2 shown in the analysis than can be accounted for as kaolinite, quartz and amorphous silica, but the excess is less than in the superfine fraction. Diffraction diagrams of material after sodium sulphide-oxalic acid treatment and heating to 510° C. showed some quartz and mica lines. In the presence of these lines it is impossible to see whether or not any of the hk0 lines of montmorillonite, found on corresponding diagrams of the superfine fraction, are present. If this mineral is present, the base exchange capacity, dehydration and chemical data show that its amount is less than that in the superfine fraction. The composition of this fraction seems to be 50% kaolinite, 15% mica, 10% oxide and hydroxide of iron, 3% of quartz and possibly up to 15% of a member of the montmorillonite group.

RED CLAY COARSE FRACTION

This fraction differs from the fine clay only in having more quartz and slightly more mica. An estimate based on the principles outlined above gives kaolin or halloysite 40%, mica 30%, quartz 10%, iron oxide and hydroxide 5–10%. There is no reason to assume the presence of a member of the montmorillonite group in this fraction.

The results of the estimates for all six fractions are summarized in Table VII.

Table VII. *Minerals present in fractions of clay as percentage of fraction*

	Black cotton soil, 12–18 in.			Red earth, 18–24 in.		
	Coarse	Fine	Superfine	Coarse	Fine	Superfine
Beidellite	30	70	90	—	(?) 15	(?) 30
Kaolinite	15	10	—	40	50	60
Mica	15	15	—	30	15	—
Quartz	30	5	—	10	3	—
Hematite and goethite	5	—	—	8	10	10

DISCUSSION

The red and the black soils under investigation are derived from the same or from very similar rocks, and as they occur near each other they are exposed to the same climatic conditions. The differences in the mineralogical compositions of the two clays must therefore be due to processes resulting from the difference in the topographical position of the two soils, the red soil occurring on a slope of waste land, while the black soil is found in the plain in an irrigated area. According to Desai (1939) it is a general experience that red soils in the vicinity of black cotton soils are only found on slopes. There are many indications showing that the red soil is eluvial, being strongly leached, whereas the black soil is illuvial, receiving leaching products. The percentage of particles above 2 mm. is very high in the red soil, and the silt and clay contents are comparatively low. Both conditions are reversed in the black soil, and a large proportion of its particles above 2 mm. consist of secondary formations, carbonate concretions. Relatively high proportions of felspar and hornblende are found in the fine sand fractions of the red soil, but these minerals have almost disappeared from the black soil. The red soil has a lower pH than the black one, especially in the top layer. The data given in this study show that under such eluvial conditions kaolinite or halloysite is the main constituent of the clay, whereas in the illuvial

black soil a member of the montmorillonite group predominates in the clay. Correns & Engelhart (1938) have shown that the weathering of felspar is a molecular process and that the rate at which alumina and silica are dissolved depends within certain limits on the acidity of the leaching solution. Which secondary minerals are formed, and where they are formed in nature will largely depend on the conditions of drainage and on the type and amount of other ions, mainly alkalies and alkaline earths, present.

Kaolin and montmorillonite have been synthesized in hydrothermal bomb experiments and the conditions of their formation investigated. According to Noll (1936) the amount and type of alkalies and alkaline earths present and the pH are of greater importance than the relative amounts of silica and alumina, and under appropriate conditions both minerals are formed together. Kaolin formation is favoured by acid or neutral conditions and montmorillonite formation by alkaline conditions. Although hydrothermal bomb experiments are not directly comparable with surface weathering and the formation of clay minerals, it is noteworthy that the montmorillonite and kaolinite occur in soils of types investigated here under just those conditions of reaction under which they have been produced in the laboratory. The simplest hypothesis is that in nature they are produced in a similar manner.

It has been shown in the description of the superfine red clay that kaolin is not the only clay mineral present and that there was possibly 20–30 % of a material which may be beidellite or perhaps a silicate not known as a mineral, capable of forming beidellite. This mineral decreases in amount as the particles become larger. Such material would, on account of its small size, be easily transported and might form beidellite under the conditions prevailing in the black soil.

Mica in the red clay decreases rapidly with decreasing grain size, probably indicating its instability under the conditions prevailing in the red soil. In the black soil it is absent from the superfine fraction, but occurs in about equal proportions in the fine and coarse clay. The quartz percentage of the coarse black clay is quite high, but it is impossible to say whether this quartz is residual or newly formed. There is no direct microscopic evidence for secondary quartz in the coarse clay or in the silt fraction of the black soil, which consists almost entirely of quartz. Kaolin occurs in minor amounts in the coarse and fine black clay, but not in the superfine fraction. It seems likely that this kaolin was transported from the red soil and not formed in the black soil, as in the latter case it would probably not decrease in amount with decreasing grain size.
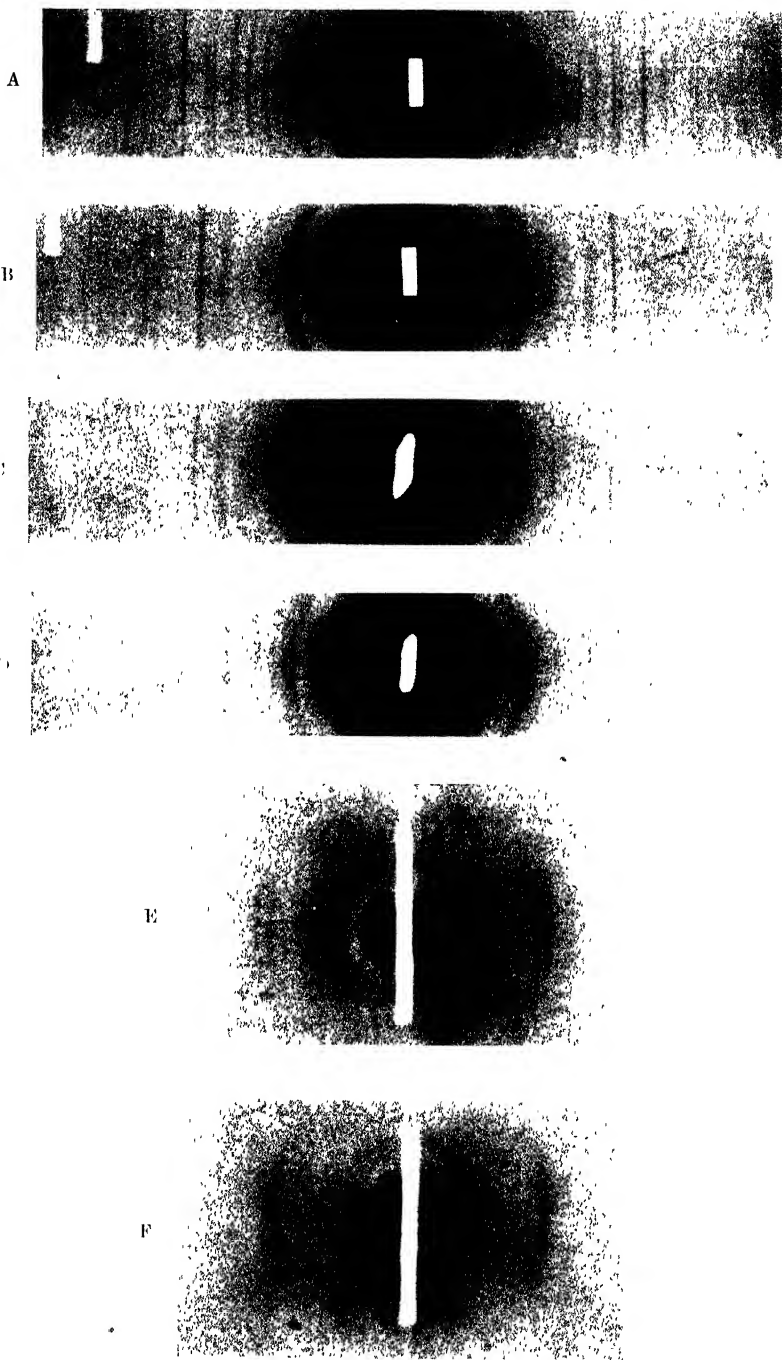
X-ray diffraction diagrams of clay fractions. A to D, powder diagrams, E and F aggregate diagrams

A. Black cotton soil, coarse clay.
B. Black cotton soil, superfine clay.
C. Red earth, superfine clay.
D. Red earth, coarse clay.

E. Black cotton soil, fine clay.
F. Red earth, fine clay.

(For reproduction the blackening in the centre has been reduced by partial shading.)

Summary

. The mineral compositions of the clays from a red earth and a black cotton soil from Hyderabad, Deccan State, India, occurring in close proximity in the field are determined. Both soils are derived from the same or from very similar parent rocks, a coarsely crystalline granite or gneiss.

For both soils there is practically no variation in the mineralogical composition of the clay throughout the profile, but for any given clay there is some variation with grain size. The main contrast between the two is that the red clay contains predominantly kaolinite or halloysite, whereas the black clay contains mainly beidellite, a member of the montmorillonite group. The topography appears to be the principal factor associated with this difference in minerals, and the processes of weathering believed to have produced the contrasted clays are discussed with reference to experiments on the leaching of felspar in the laboratory and on hydrothermal synthesis.

REFERENCES

Correns, C. W. & Engelhardt, W. v. (1938). *Chem. d. Erde*, **12**, 1.

Correns, C. W. & Mehmel, M. (1936). *Z. Kristallogr.* **94**, 337.

Denison, J. A., Fry, W. H. & Gile, P. L. (1929). *Tech. Bull. U.S. Dep. Agric.* no. 128.

Desai, A. D. (1939). Thesis, University, Aberdeen. To be published as Bulletin of the Dept. Agric., Hyderabad.

Drosdoff, M. & Truog, E. (1935). *J. Amer. Soc. Agron.* **27**, 312.

Grim, R. E., Bray, R. H. & Bradley, W. F. (1937). *Amer. Min.* **22**, 813.

Grim, R. E. (1939). *J. Amer. Cer. Soc.* **22**, 141.

Hendricks, S. B. & Alexander, L. T. (1939). *Soil Sci.* **48**, 257.

Kelley, W. P., Dore, W. H., Woodford, A. O. & Brown, S. M. (1939). *Soil Sci.* **48**, 201.

Larsen, E. S. & Wherry, E. T. (1917). *J. Wash. Acad. Sci.* **7**, 213.

Nagelschmidt, G. (1938). *Min. Mag.* **25**, 140.

—— (1939). *J. agric. Sci.* **29**, 477.

Noll, W. (1936). *Min. Petrogr. Mittlg.*, **48**, 210.

Parker, F. W. (1929). *J. Amer. Soc. Agron.* **21**, 1030.

Raychaudhuri, S. (1936). Thesis, University, London.

Robertson, I. M. & Shewan, J. M. (1935). *J. Soc. Chem. Ind., Lond.*, **54**, 35.

Ross, C. S. & Kerr, P. F. (1934). *Prof. Pap. U.S. Geol. Surv.* **185**, 9.

Toth (1939). *Soil Sci.* **48**, 385.

Truog, E., Taylor, J. R., Pearson, R. W., Weeks, M. E. & Simonson, R. W. (1937). *Proc. Soil Sci. Soc. Amer.* **1**, 101.

PRELIMINARY EXPERIMENTS ON THE ESTIMATION OF TRACES OF HETEROAUXIN IN SOILS

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INTRODUCTION

MANY recent experiments have shown the value, at least under certain circumstances, of the application of growth-promoting substances to plants, in increasing yields, in enhancing disease resistance of seedlings, in promoting the rooting of cuttings, etc. In view of this work, it is plainly of importance to know whether appreciable quantities of these active substances are normally present in soil, and if so, what quantities occur and what changes they are subject to in the course of nature, or under the various operations of tillage, etc. In practical application the substances used have hitherto always been heteroauxins,[1] and since the substances are readily prepared synthetically at a reasonable price, some of them have already found commercial application; the present work has therefore been confined to the heteroauxins, and no data have been collected regarding whether the results obtained apply also to the true auxins,[1] or whether these latter substances may not also occur in soils and be effective in the tests for heteroauxins which will be described.

Nor has account been taken of the effects exerted by the electro-positive phytohormones such as aneurin, though it would be of interest to know whether these substances occur in any amount in normal soils.

As far as the writer has been able to ascertain, no previous investigator has attempted to determine the quantity of plant hormones existing in soils, though the possible importance of the matter had been commented on as far back as 1933 by Hardy (1933). On the other hand, there is a copious literature on the production of phytohormones by soil micro-organisms *in vitro*, from which one may assume that there must be at least some indolyl acetic acid, and probably other hormones, present in non-sterile soil. The principal previous contributions to this

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[1] *Definition*: By a heteroauxin is meant any aryl-substituted lower fatty acid which has been shown to be active in at least one of the recognized tests for growth promoting activity. By a true auxin is meant one of the two acids, auxentriolic or auxenolonic. β-Indolyl acetic acid is the only heteroauxin known to occur in nature.

aspect of the question are summarized by Roberts & Roberts (1939), who themselves report investigations on some 150 cultures of micro-organisms isolated from soils, in which they found that many bacteria and actinomycetes could produce auxins (they did not distinguish between auxins *a* and *b* and heteroauxin) both on natural and synthetic media, but that the fungi which they tested could produce them only on beef-extract peptone agar, not on a synthetic medium. All the work on the production of auxins by micro-organisms has depended upon the various testing methods using growth responses of plant organs, especially the *Avena* test of Went, which do not give results which can be strictly interpreted in terms of the actual amount of growth substance produced, and are subject even in their own terms to a considerable error; furthermore, no attempt has been yet made to determine whether, and if so how, micro-organisms produce growth hormones under the conditions actually prevailing in soils.

The previous work on the subject of the presence of heteroauxin or other plant hormones in soil is therefore too fragmentary and uncertain to have any practical bearing on horticulture or agriculture. The present investigation is an attempt in a tentative and altogether preliminary way to remedy this; and also to throw some light on the biology of the bacteria and fungi of the soil. These organisms form a fairly definite ecological entity, and it is probable, from the work of Roberts & Roberts, that the production of heteroauxin in the soil would provide a valuable index of the state of activity of this association, the importance of which in all branches of agriculture can hardly be doubted.

METHODS OF ESTIMATION

Preliminary considerations

The quantities of heteroauxin present in normal soils are too small for detection by the methods hitherto in use, let alone for quantitative determination. In order to carry out such determinations, therefore, it would be necessary either to devise some means of chemical concentration of the heteroauxins or to invent a method of estimating the active substances sensitive enough for the purpose. The latter was the course adopted in the present work.

That this might be possible was suggested by the results of Bonner & Koepfli (1939), who found noticeable inhibition of root growth by indolyl acetic acid at concentrations as low as 1 part per billion (1 billion $= 10^{12}$), and more particularly by various workers who have

reported optimal concentrations of this substance for the root growth of various plants, e.g. Fiedler (1936) with *Zea mays*, Amlong (1936) with *Vicia faba*, and Thimann (1937) with *Pisum* spp. In all these cases, the optima reported were of the order of 10^{-10}. The results reported in the present paper suggest a much lower optimum in the case of wheat; the discrepancy may be due to a difference in experimental technique.

In order to use any such effect for the purpose of estimating indolyl acetic acid in solution, it would be necessary to reduce it to such a form that the dependence of magnitude of the effect measured on the concentration of the solution could be so accurately determined that the experimental error of the estimation should be reasonably small. This would be best done by finding some easily measured physical characteristic of the experimental plants affected by the hormone treatment; with this end in view, having regard to the results of Heyn (1931) and others on the effect of heteroauxin on the cell walls of the *Avena* coleoptile, experiments were made to investigate the extensibility of the tissues of the roots of wheat seedlings after treatment with dilute solutions of indolyl acetic acid. In these experiments short sections of the root taken from just behind the tip were measured in length by means of a micrometer eyepiece, first in a condition of plasmolysis, and then after 20 hr. immersion in distilled water. Any increase in extension observed in treated roots over the controls might then be attributed either to a decrease in the modulus of elasticity, or to an increase in the force causing extension, in this case provided by the osmotic pressure, or to a combination of both factors. The results obtained were as follows: first, Table I shows the results of typical experiments.

Table I. *Effect of indolyl acetic acid on extensibility of root tissue*

Treated in: ...	Distilled water	Indolyl acetic acid	
		10^{-12}	10^{-8}
1st Exp.: Percentage elongation	4·88	10·3	9·64
Standard deviation	2·0	2·0	2·0
2nd Exp.: Percentage increase in diameter	4·09	8·18	3·45
Standard deviation	1·7	1·7	1·7

Similar results were obtained in other experiments of a similar kind; it will be observed that significantly greater extension takes place in roots treated in 1 p.p.b. indolyl acetic acid in both cases, but that the more concentrated solution gives divergent results. In order to obtain more information on this effect, experiments were made to determine whether any increase of osmotic pressure took place in the treated roots.

For this purpose, the only cells whose osmotic pressure can be determined *in vivo* are the root hairs and the sloughed-off cap cells, in which plasmolysis can be readily observed. Of these the former, being directly concerned with the vital functions of the plant, were selected for observation.

Effect of indolyl acetic acid on osmotic pressure

Two methods of measuring the osmotic pressure were attempted: by immersing a series of roots in solutions of sucrose having various osmotic pressures, and noting the minimum concentration necessary to induce plasmolysis; and by immersing a single root in a solution known to be hypertonic, and noting the length of time elapsing before plasmolysis becomes evident. With a little practice it was fairly easy to determine the moment when any given root hair first showed a space between the protoplast and the cell wall at the tip, and it was found that a majority of the hairs in any given stage of development on one root would show plasmolysis within a range of about $\frac{1}{2}$ min. The former method has the disadvantage that a number of roots are required, and that it takes a long time to carry out a proper test, though theoretically it should be possible to obtain a fairly high standard of accuracy by it. The second method, which is very well adapted to making many tests (on, say, a series of roots treated in different ways) in a short time, has the disadvantage that, even if it were possible accurately to calibrate the plasmolysis delay against actual osmotic pressure, the accuracy of the measurement of the delay is scarcely more than about 1 min. in a total of up to 10 min. so that it is useful only as a qualitative indication of difference of osmotic pressure.

A preliminary experiment using the first method showed that the osmotic pressure of root hair cells which had been immersed overnight in distilled water was 6.5 ± 5, while that of cells on roots treated in 1 p.p.b. indolyl acetic acid was 8.5 ± 5 atmospheres. A more detailed experiment gave the results shown in Table II. It will be observed that, in addition to a general diminution of the osmotic pressure at the higher temperature, treatment with indolyl acetic acid at 10^{-12}, but not at other concentrations, produces a definite increase of the pressure.

Further experiments were made, in which the plasmolysis delay method was used. In using this method, the practice was to take a pair of roots (usually the first two laterals from a seedling), to treat one with the experimental solution and the other with distilled water by immersion in a Van Tieghem cell overnight, and in taking the readings, to immerse

Table II. *Effect of indolyl acetic acid on osmotic pressure of root hairs*

Logrecip of concentration of indolyl acetic acid	Osmotic pressure of root hair cells treated overnight at	
	Room temperature	25° C.
∞	5·5	5·0
12	7·5	6·5
11	6·0	5·0
10	6·0	(?) 5·0
9	5·5	5·0
8	<5·0	<4·0

both at the same time, as near as could be, in the hypertonic solution (also in a Van Tieghem cell); the control root was then kept under observation until plasmolysis became evident in a majority of the hairs, and then the treated root was brought under the microscope. The time was noted (*a*) on applying the plasmolysing solution, (*b*) when the control root plasmolysed, and (*c*) when the treated root plasmolysed; these readings were made accurate to $\frac{1}{2}$ min. The object of the first experiments made with this method was to determine, as accurately as possible, the optimum concentration of the hormone for the osmotic effect so that it might be used as a criterion in the quantitative estimation of the active substances in soil. The results obtained are given in Table III.

Table III. *Experiments to locate the optimum concentration of indolyl acetic acid for increase of osmotic pressure*

Concentration of indolyl acetic acid in p.p.b.	Experiment no.				
	I	II	III	IV	V
	(difference in plasmolysis delay, treated-control, min.)				
0·40	6	½	4	1½	2¼
0·38	—	—	—	2½	>8
0·36	—	—	—	5¼	2¼
0·35	>12	3½	Neg.	10	Neg.
0·34	—	—	—	5	2
0·33	—	—	—	? 3½	2
0·32	—	—	—	2½	?
0·30	1	Neg.	2	1	0
0·25	0	? 2	—	—	—
0·20	½	0	—	—	2½
0·18	—	—	—	—	7
0·16	—	—	—	—	6¼
0·15	>13½	4	—	—	?
0·14	—	—	—	—	<3
0·12	—	—	—	—	0
0·10	1¼	0	—	—	1
0·05	0	½	—	—	—

In interpreting these figures, it should be noted that the magnitude of the differences observed is greatly affected by a number of factors,

such as temperature during treatment, age of roots used, etc., which are constant for any one experiment, but which vary from one to another. The strength of the plasmolysing solution was 8 atm., except in Exp. II, where it was 6 atm. The indolyl acetic acid solutions used in Exps. III and V was more than 24 hr. old, and it is known that the hormone decomposes in aqueous solution below pH 7, so that the apparent optima for these experiments are higher. This is probably also the explanation of why the earlier experiments gave an effect at 1 p.p.b., since these experiments were performed with a solution made up over 2 months previously.

It will be observed that, judging from the fresh solutions, there are optima at 0·35 p.p.b., and also 0·15 p.p.b.; the two optima in Exp. V maintain the same ratio of concentration. That there should be two such optima is somewhat surprising, but that this is in fact the case has been confirmed by other tests on the same lines as the above, which are reported below, and also in very numerous experiments to determine the heteroauxin content in soil samples, in which the two optima both frequently appear.

It will be further observed that, as exhibited by the plasmolysis delay method, the optima are sufficiently sharp to be determinable to within less than 3 %, and could thus be used as a means of estimating the quantity of active substance present in any given solution, by determining what dilution of the solution gives the optimum effect, and equating this dilution with 0·35 (or 0·15) p.p.b. It would, of course, be necessary to perform preliminary pilot experiments to determine the proper range of dilutions to investigate more accurately, and also which of the two optima is which.

Effect of non-optimal concentrations of indolyl acetic acid

It should be stated here that experiments were made to find out whether any higher optima might exist, above the two shown in the table. These experiments investigated solutions up to 1·0 p.p.b. and no higher optima were found. Experiments were also made to ascertain whether, at any concentrations of indolyl acetic acid, the osmotic pressure of the hairs of the treated roots might be reduced in comparison with the controls.

These diminutions of osmotic pressure might easily be overlooked, using the technique described above, because in these cases the root examined first will be expected to take longer to show plasmolysis than the other, so that the observer will be unable to say whether the second

root was not, as sometimes happens, in an abnormal condition from the start. Furthermore, the magnitude of the negative effect, even if it in fact occurs, might be too small to enable it to be detected by the plasmolysis delay method.

To overcome these difficulties, experiments were performed in which the order of the observations was reversed, and in order the better to show up relatively small effects, the osmotic pressure of the plasmolysing solution was made 6 atm. instead of 8 atm. as was customary. In these experiments the regions of absolute concentration around 0·05 and 0·25 p.p.b. were investigated, and also the optima already found by way of controls. A typical experiment is shown in Table IV. It will be observed that the significant differences in plasmolysis delay were observed at the expected points; their significance was, in these experiments, confirmed by a comparison with the state of plasmolysis exhibited by the root first examined when the second root was just beginning to show it; this procedure showed up the fact that the treated root hairs at the "pessimum" concentrations frequently plasmolysed, once they had begun, with considerable rapidity.

Table IV. *Results of an experiment to demonstrate the reduction of osmotic pressure*

Concentration of indolyl acetic acid in p.p.b.	Time of immersion in solution	Delay in plasmolysis		Difference
		Treated	Control	
0·35	10·10	>8	<8	Neg. (opt.)
0·27	10·22	2*	3	1†
0·25	10·27½	1	5?	4? (pes.)
0·23	10·37	3	5	2†
0·15	10·44½	>7	<5½	Neg. (opt.)
0·06	10·53½	2½*	5	2½†
0·05	11·00½	2½*	5	2½† (pes.)
0·04	11·08	2	3½	1½

* Indicates that the material plasmolysed with great rapidity.
† Indicates that the difference may be considered significant. (That the magnitude of the differences observed is less than with, say, the experiments set out in full in Table VI is to be accounted for by the lower osmotic pressures involved.)

Other experiments performed in repetition of this substantially confirmed the results obtained. The application of these results to the design of pilot experiments in estimating the heteroauxin content of soil samples, etc., also affords confirmation of the existence of these pessima.

The sensitivity of the plasmolysis delay method of detecting osmotic pressure differences is not sufficiently great to locate the zero points to be expected midway between the optima and pessima.

The observations described above, if correct, provide the basis for

a more rational design of pilot tests intended to locate roughly the position of the optimal concentrations in terms of a given arbitrary solution, which problem is of importance in the practical application of the method in estimating the active substance.

If the region of concentrations included by the two optima is covered by five arbitrary concentrations, equally spaced on a logarithmic scale, then it is desired to choose these five concentrations so that not more than four shall lie on or near points of zero effect. This will be achieved if the ratio of adjacent concentrations is made equal to the cube root of the ratio between the said optima, namely $\sqrt[3]{7/3}$, or approximately 1·326. In this case the most unfavourable possible distribution of the concentrations about the two optima will be when the first and second, fourth and fifth lie on either side of the optima, and the third lies at the intervening pessimum; provided care is taken in the observations to locate the pessima as well as the optima this should serve to determine what range of concentrations should be taken in the more accurate tests. The number of test concentrations required to cover a given range R will be given by $\log_{1·33}(R)$.

In practice, the ratios will not need to be accurately 1·33, and for convenience of making up the solutions, the series of concentrations in the ratio 6 : 9 : 11 : 14 : 20 : etc., was arrived at. In the use of this series, extended as might appear necessary, it was found that the interpretation of the results on the above basis always led to a correct location of the optima.

What is the nature of the active substance in soil?

In applying this method to the actual estimation of heteroauxin in soil, the question arises as to whether substances other than the heteroauxins can produce this effect. This question can never be fully answered until a large number of possible rivals of indolyl acetic acid in this respect have been tried out, but it may be regarded as unlikely that many substances should be capable of exerting so marked an effect at so great a dilution. But it is nevertheless desirable to identify at least to within certain limits the substances which are responsible for the osmotic effects exerted by extracts of ordinary soils. To this end the following experiment was performed.

10 c.c. of a soil extract, prepared by stirring thoroughly 30 c.c. of distilled water with 30 g. of a soil sample previously dried for 20 hr. at 95° C., and filtering, were shaken three times with separate portions of 10 c.c. of ether. The combined ether portions were divided into two parts

equal in volume; the first was then shaken three times with 1 % potassium carbonate solution, and then twice with distilled water; the second was shaken twice with distilled water only. Both ether portions were then evaporated under reduced pressure to a small volume, and the evaporations completed over 5 c.c. portions of the original extract. Air was then passed slowly through these two portions of treated extract under somewhat reduced pressure to remove the last traces of ether. Both portions were then tested for their content of active substance by the methods described, with the results shown in Table V. From this it appears that the active substance is soluble in ether more readily than in water, and that it is removed by treatment with potassium carbonate, i.e. that it is an acid. These are properties of indolyl acetic acid, and of heteroauxins in general, and while it cannot be said that this experiment serves to identify the substance it gives a certain indication, concordant with the hypothesis that the substance present in soil which is active in these tests is indolyl acetic acid. This will be assumed hereinafter.

Table V

Treatment	Optimum concentration (upper) in terms of original solution	Equivalent quantity of indolyl acetic acid in the soil sample (γ/kg.)
Ether washed with K_2CO_3	—	0
Ether washed with water only	$3 \cdot 3 \times 10^{-3}$	0·11
Solution untreated	$3 \cdot 3 \times 10^{-3}$	0·11

TECHNIQUE USED TO ESTIMATE HETEROAUXIN IN SOIL SAMPLES

Before proceeding to describe the results obtained in investigating the effect of certain factors on the heteroauxin content of various soils, details will be given of the procedure adopted in making the estimations, together with such special precautions as appeared necessary, with the reasons for their adoption.

The soil samples taken from the field according to the usual technique, or portions of soil subjected to laboratory treatments of various kinds, were dried overnight at 120° C. in an oven. They were then ground to the fineness of fine dust in a mortar, and any stones and solid organic debris were removed, if necessary, by means of a fine sieve. In this state the samples could be stored for at least a month (longer intervals were not investigated) without appreciable change in the content of active substances.

The extracts were prepared by adding to a portion of the soil sample an equal weight of distilled water, stirring thoroughly, and filtering. It appeared that only an insignificant fraction of the total indolyl acetic acid was held by adsorption or otherwise in the soil, so that repeated extraction was not required. After preparation of the extract, its pH was measured by means of a capillator, using brom-thymol blue as an indicator. If the pH was less than 6·8, the solution was diluted immediately with tap water in the required proportions; otherwise this precaution was not considered necessary, provided the solutions were not kept more than a few hours before dilution. Dilution was always performed with tap water for two reasons: (a) any effect due to the different mineral content of different soils was probably thus eliminated, since in the dilutions found necessary at least 99% of the mineral content of the diluted solutions would then be due to the tap water only; and (b) the tap water had sufficient buffering action to keep the diluted solutions always at pH 7·1–7·2, which both reduced and equalized the tendency of the active substances to decay during the experimental period.

In the preliminary pilot test to determine what range of dilutions to subject to closer investigation an arbitrary range of fairly widely spaced dilutions was employed. In later experiments the dilutions adopted were in the ratio 6 : 9 : 11 : 14 : 20 : 26 : 35 : 47 : 60. The reasons for this particular choice have been given above. It was found that using such a series of dilutions it was generally possible to locate both optima with sufficient accuracy to proceed at once to the accurate investigation. In this latter part of the test a series of dilutions differing by not more than 10% was taken.

In most tests, seven or eight dilutions were used. Each diluted solution was placed in one of two Van Tieghem cells on a slide, the other containing tap water. Into each cell was then placed one of the two lateral roots of a wheat seedling grown in a Petri dish at room temperature on a piece of wet filter paper. Great care was taken in selecting the roots used. They were taken only from plants of wholly normal appearance, had to be not less than 5 mm. and not more than 20 mm. long, had to be as nearly equal in length as could be judged by eye, and were preferably free from marked twists or irregularities. First laterals were preferred, but second laterals were found satisfactory, though they less frequently fulfilled the above specifications. After introducing the roots, the cells were sealed with coverslips, and made airtight with vaseline, to prevent evaporation. Great care was also taken in all manipulation of the roots, to avoid damaging the root hairs. They were severed with a sharp razor,

and touched only at the basal end with forceps; they were not decapitated; this precaution was found to be unnecessary, and to involve almost always injury to the hairs. Although the root tips, according to the results of Fiedler (1936) with *Zea mays*, contain some auxin, the substance appears not to diffuse into the cortical cells, and no evidence of its effect on the root hair cells has yet been found.

The cells containing the roots under treatment were kept in the laboratory overnight, covered from direct sunlight (which was found to be detrimental to the root hairs) and subjected to examination in the morning. The cells were then emptied with a nipple pipette, and refilled with the plasmolysing solution. The time of doing this was noted. Care was taken that the surface of the plasmolysing solution exhibited a regular meniscus, since otherwise surface forces would make it difficult to prevent the root from moving when under observation, and also because the optical distortion, resulting when this precaution was neglected, made accurate observation of the root hairs difficult. The slides were then placed under the microscope, in which a $\frac{2}{3}$ in. objective and a $10 \times$ eyepiece were employed.

The control root was observed first, since this was expected to plasmolyse, if anything, earlier than the treated one. As soon as a majority of the hairs showed a distinct space between plasma and cell wall at the tip (the tip was frequently thickened) the time was again noted, and the treated root brought under observation.

It was commonly found that, even if the two roots plasmolysed at the same time, an interval of some $\frac{1}{2}$ min. was recorded between them, owing to the difficulty in picking up the root hairs with the eye when first focussing upon them. As this personal factor was constant, and not much diminished with practice, no account was taken of it in recording the results; that it was a real effect was shown by those experiments in which the order of the observations was reversed, in which the control roots appeared to plasmolyse later. This factor was insufficient to mask the effect due to a significant difference in osmotic pressure between the control and treated roots, whether positive or negative.

In order to show what kind of observations were made in these tests, the complete investigation of one of the earlier soil samples investigated will be given in the form in which it was entered in the experimenter's notebook (Table VI). It will be observed that three accurate tests were made after the initial pilot test. This was the usual practice, the last test being made after a lapse of a week or two.

Table VI. *Sample C*

pH of extracts: 7·1 ±0·05. Sample taken 23. ii. 40; dried 23–24. ii. 40

Concentration in terms of original solution	Time of immersion	Delay of plasmolysis (min.)			Remarks
		Control	Treated	Difference	
Test I (2. iii. 40)					
6·0 × 10⁻³	10·02¼	3	<3	<0	
4·0 × 10⁻³	10·20	4	6½	2½	
3·0 × 10⁻³	10·30	2	6½	4½	Optimum about here
2·0 × 10⁻³	10·39	2½	4½	2	
1·5 × 10⁻³	10·47¼	2	c. 5	c. 3	Possibly lower optimum
1·0 × 10⁻³	10·55	2	4	2	
0·75 × 10⁻³	11·02	c. 6	7	c. 1	
0·5 × 10⁻³	11·11¼	Both more than 10		?	
Test II (5. iii. 40)					
4·0 × 10⁻³	10·48	2	2½	½	
3·7 × 10⁻³	10·52	3½	<3½	<0	
3·5 × 10⁻³	10·57	c. 2⅔	c. 3	c. ⅓	Poor material
3·3 × 10⁻³	11·03	2	6*	4	Optimum (* perhaps more)
3·1 × 10⁻³	11·13¼	<1¼	c. 3	<3	
2·9 × 10⁻³	11·21	2	3	1	
2·7 × 10⁻³	11·26	2	3	1	
2·5 × 10⁻³	11·30½	3	5½	2½	
Test III (7. iii. 40)					
4·0 × 10⁻³	9·53½	3	<3	<0	
3·7 × 10⁻³	9·58½	1	2½	1½	
3·5 × 10⁻³	10·03	1½	2	½	
3·3 × 10⁻³	10·07¼	1½	7½	6	Optimum
3·1 × 10⁻³	10·18	1½	1½	0	
2·9 × 10⁻³	10·23½	4	<4	<0	
2·7 × 10⁻³	10·31	<3	c. 5	c. 2	
2·5 × 10⁻³	10·38	1½	1½	0	
Test IV (1. iv. 40)					
3·9 × 10⁻³	11·27	2	4	2	
3·7 × 10⁻³	11·33	4	4	0	
3·5 × 10⁻³	11·39	2½	3	½	
3·3 × 10⁻³	11·43½	2¼	>6½	>4	Optimum confirmed
3·1 × 10⁻³	11·52	4	4*	0	* Poor material
2·9 × 10⁻³	11·59½	3	c. 4½	c. 1½	
2·7 × 10⁻³	12·06½	2	3½	1½	

Conclusions. $3\cdot3 \times 10^{-3} \times$ original extract is equivalent in activity to $3\cdot5 \times 10^{-13}$ indolyl acetic acid: therefore, assuming activity is due to this substance, concentration thereof in original extract is $3\cdot5/3\cdot3 \times 10^{-10}$, that is to say: *0·106 ±0·003 γ per litre* (or the same quantity per kilogram of dried soil).

Sources of error

There appear to be a number of sources of error in the above methods. First, it has been shown that the effects described are produced by β-indolyl acetic acid, having the structural formula
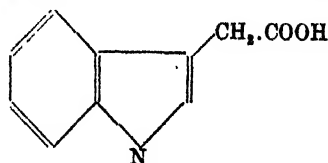
but whether other substances are capable of exerting the effect is quite unknown, and despite certain *a priori* considerations suggesting that it must be fairly specific, we cannot yet confidently assert that the citing of results in terms of so much of the substance is fully justified.

Secondly, it may be that in the course of the drying out of the samples, though done as quickly as possible without using too high temperatures, a certain amount of the hormone is destroyed. This error may perhaps be considerable, though systemic.

Thirdly, there may be small error, also systemic, due to the incomplete elution of the hormone from the soil samples.

Possibilities of improvement

The accuracy of the method might be increased by growing the experimental seedlings under controlled conditions of temperature, illumination, etc., and by observing rigorous aseptic precautions, though no evidence has been obtained that any quantity of the hormone is produced by fungal or bacterial growth on the roots in the present experiments. By the use of a more accurate method of determining the osmotic pressure, and perhaps by amplification of the results by the use of statistical methods, it might be possible to increase the accuracy with which the optimum could be located. Finally, methods might be devised for overcoming the second and third of the sources of error listed above, such as rapid air-drying of the samples, and the repeated washing of the material before testing for the activity of the solutions. The accuracy claimed for the present work is not more than 3 %, but this might well be increased in this way to less than 1 %.

EXAMPLES OF THE APPLICATION OF THE METHOD

(1) *Effect of various manurial treatments of the soil*

Materials.

In order to ascertain in a general way what quantities of heteroauxin might normally be present in agricultural soils, and what range of variation they might exhibit, estimations were made of the heteroauxin content of a series of soil samples taken from an experiment laid out in the Plantations of the Long Ashton Research Station, designed to obtain information of the effect of different manurial treatments on the growth of black currants. The currant bushes were planted 6 ft. apart in square formation and the intervening ground was cultivated. The treat-

ments which were in triplicate and distributed in randomized blocks were as follows:

A. No manure applied.

B. Dung, 10 tons per acre.

C. Complete artificials, comprising superphosphate 3 cwt. per acre, nitrate of soda 4 cwt. per acre, sulphate of potash 3 cwt. per acre.

D. Complete artificials with the nitrate of soda omitted.

E. Ditto, with the superphosphate omitted instead.

F. Ditto, with the sulphate of potash omitted instead.

The samples were taken from the first three replicates of each treatment; all plots were randomized. The sampling was done by means of an auger, taking the surface 9 in. The samples were taken on the morning of 23 February; the weather was warm and bright, coming after a somewhat wet period. The spring of 1940 was rather late, owing to the severe winter. The samples were dried at about 120° C. that night, and pulverized the next morning.

During the succeeding weeks the samples were examined by the methods described and the results were noted in the form shown in the case of sample "C" in the last section.

Results.

The results of these estimations, expressed in γ of indolyl acetic acid per kilogram of dried soil, were as follows:

Samples from treatment	γ heteroauxin per kg.
A. No manure	0.075 ± 0.002
B. Dung	0.200 ± 0.006
C. Complete artificials	0.106 ± 0.003
D. Lacking nitrogen	0.092 ± 0.003
E. Lacking phosphorus	0.092 ± 0.003
F. Lacking potash	0.062 ± 0.002

From this it may be tentatively surmised that a deficiency in potassic manuring has tended to depress the quantity of heteroauxin in the soil, and it seems fairly clear that the dung treatment considerably increased it.

(2) *Effects of sterilization*

Sterilization of soil is frequently observed to produce a certain stimulan of plant growth, independently of any effect due to the destruction harmful organisms; experiments were therefore made to determine pther any change occurs in the heteroauxin content of soil when jected to sterilization sufficient to be a contributory factor in this ct.

Materials.

In these experiments, the soil used was a mixture of ordinary field soil obtained from the plantations belonging to the Long Ashton Research Station, and leaf mould; such materials are very commonly used for potting plants, etc., in horticultural practice. The mixture was made up immediately before the commencement of each experiment, and the same lot of soil was used throughout any given experiment.

In the first experiment a sample of the soil was taken and subjected to sterilization by steam for 2 hr.; one portion was kept thereafter in the airtight vessel in which it had been sterilized, for 6 days, and then dried and tested for indolyl acetic acid by the methods described. A second portion was dried immediately after sterilization, and a third was exposed to the air in the greenhouse for 6 days, in a shallow wooden seed-box, and watered daily as though it contained seeds. In the second experiment the soil was sterilized in an autoclave at 10 lb. pressure for $\frac{1}{2}$ hr.

Results.

On estimating the quantities of heteroauxin present in the three portions from the first experiment, the following results were obtained:

Table VII

Treatment	Quantity of heteroauxin (γ indolyl acetic/kg.)
Sterilized and sampled immediately	$0 \cdot 042 \pm 0 \cdot 001$
Sterilized and sampled after 6 days sterile	$0 \cdot 034 \pm 0 \cdot 001$
Sterilized and sampled after 6 days exposed	$0 \cdot 146 \pm 0 \cdot 005$

In the second experiment, the soil was exposed after sterilization for a varying period, and a portion of the freshly made up, but untreated, soil was tested by way of a control. The results were as follows:

Table VIII. *Effect of exposure to infection on the heteroauxin content of sterilized soil*

Period of exposure hr.	Quantity of heteroauxin (γ indolyl acetic/kg.)
0	$0 \cdot 016 \pm 0 \cdot 0005$
$19\frac{1}{2}$	$0 \cdot 039 \pm 0 \cdot 001$
$43\frac{1}{2}$	$0 \cdot 038 \pm 0 \cdot 001$
$69\frac{1}{2}$	$0 \cdot 037 \pm 0 \cdot 001$
$115\frac{1}{2}$	$0 \cdot 039 \pm 0 \cdot 001$
Untreated soil	$0 \cdot 175 \pm 0 \cdot 005$

It can be inferred from the results given in the last two tables that sterilization, especially of the rather more severe character used in the

second experiment, tends to depress the amount of indolyl acetic acid present by up to 90% of the original amount. But from Table VIII it seems as though, after sterilization, the soil relatively quickly regains equilibrium in regard to heteroauxin content. The equilibrium value attained is not the same as the amount originally present, probably because the freshly made up mixture is not in a state of equilibrium. To ascertain how long it might take for such equilibrium to be arrived at, starting from the unsterilized fresh mixture, the following experiment was carried out.

(3) Effect of exposure to greenhouse conditions without previous sterilization

Materials and methods.

The materials used in this experiment were the same as those used in the previous experiment. The freshly mixed soil was sampled, by the usual method of rapid drying, and further samples were taken from shallow seed-boxes of this soil after exposure to greenhouse conditions with daily watering for varying intervals of time. In addition, samples were taken from the same soil after sterilization for ½ hr. under 10 lb. pressure in an autoclave, (a) immediately after sterilization, and (b) after exposure as above for about 3 days. The last sample should, according to the previous results, give the "equilibrium value" of the heteroauxin content as attained starting from a value below it. As regards the attainment of this equilibrium starting from a high value (i.e. from unsterilized soil), the figures in Table IX clearly show that it occurs.

Results.

Table IX. *Effect of exposure on the heteroauxin content of unsterilized soil*

Previous treatment	Period of exposure hr.	Quantity of heteroauxin γ/kg.
Unsterilized	0	$0\cdot071 \pm 0\cdot002$
	20	$0\cdot026 \pm 0\cdot001$
	43	$0\cdot025 \pm 0\cdot001$
	67	$0\cdot026 \pm 0\cdot001$
	114	$0\cdot025 \pm 0\cdot001$
Sterilized	0	$0\cdot010 \pm 0\cdot0003$
	67	$0\cdot025 \pm 0\cdot001$

It will be seen that, even after the short period of 20 hr., the soil has attained very nearly its final equilibrium content of the hormone, which is approximately equal to that attained by the sterilized soil, starting from a low figure.

When we compare these results with the figures given in Table VII, which show only a relatively slow disappearance of indolyl acetic acid after the completion of sterilization, when the soil was kept under sterile conditions, it becomes clear that under the conditions of the present experiment the heteroauxin is being eliminated more rapidly, that is to say, that in addition to factors tending to increase the quantity of heteroauxin present under these conditions there are other factors (probably leaching by watering) which tend to remove it. If it were possible to discourage the action of one group of factors at the expense of the other, we would thus be enabled to control, within wider limits than have been found to occur naturally in the course of this work, the amount of heteroauxin present in the soil; this offers possibilities of economic advantage, at any rate in cultivation under glass.

DISCUSSION

In order to assess the practical importance of these results, it is necessary to know what concentrations of the hormone are most favourable to the growth of plants. Previous work on this problem has taken the form of investigating the effect of applications of heteroauxins to seeds, either in solution or as dusts, and no work appears to have been done on the effect of continuous exposure of the roots of plants to hormone containing solutions, such as takes place in soil (see Croxall & Ogilvie, 1940).

Certain incomplete results of the writer suggest that there are two regions of concentration which under these conditions favour the growth of wheat plants. The upper, around 10^{-8}, manifests itself in an increased growth of the green parts, whereas the lower, 10^{-12} to 10^{-13}, increases the growth of the roots. If this is in fact the case, the concentrations actually present in soil (about 10^{-9} to 10^{-10}) are not particularly suitable.

But if it were possible, by encouraging the growth of hormone-producing (or hormone-destroying) micro-organisms in the soil, or by some other means, to raise or lower the amount present sufficiently, valuable results might ensue.

The most valuable application of the methods described, as far as they have been developed, is likely to be in throwing light on the biology of the soil micro-organisms. Furthermore there are many problems connected with the function of heteroauxin in plant physiology, hitherto obscure, which might be profitably attacked with the help of a method such as this, capable of detecting and accurately measuring such very small quantities of the active substance.

Summary

A method is described by which small quantities of indolyl acetic acid can be detected and measured quantitatively, depending on the effect of this substance on osmotic pressure of root hair cells of wheat seedlings. Full details are given of the procedure adopted and the precautions which it was found necessary to take, and suggestions are put forward as to how the method might be rendered more accurate if necessary. Possible sources of error are also discussed.

An experiment is described in which this method is used to determine what effect is produced by different manurial treatments on the content of indolyl acetic acid in the soil. It was found that farmyard manure tended to increase the quantity present.

Experiments are described in which the effect of sterilization and subsequent treatment of the soil on the content of heteroauxin was investigated. It was found that under given conditions there was an equilibrium value for the heteroauxin content which was attained in these experiments in less than 24 hr., and thereafter remained constant as long as the conditions were maintained. It was suggested that this was due to the presence of hormone-producing and hormone-destroying factors, including micro-organisms in the soil, the balance between which determined the quantity of hormone present, and which was attained in a short space of time.

In the discussion it was suggested that there are two regions of concentration in which indolyl acetic acid acting through the root system has a stimulatory effect on plant growth, in the case of wheat, at 10^{-8} (stimulating the green parts) and 10^{-12} (stimulating the roots) respectively; the quantity normally present in soil lying in the intermediate region, it was concluded that any possibility of using these results to economic advantage must wait upon the discovery of some method of controlling the quantities present in a more drastic way.

REFERENCES

Amlong, H. U. (1936). *Ber. dtsch. bot. Ges.* 54, 271.

Bonner, J. & Koepfli, J. B. (1939). *Amer. J. Bot.* 26, 557.

Croxall, H. E. & Ogilvie, L. (1940). *J. Pomol.* 17, 362.

Fiedler, H. (1936). *Z. Bot.* 30, 385.

Hardy, F. (1933). *Trop. Agric.* 10, 18.

Heyn, A. N. J. (1931). *Rec. Trav. Bot. Néerl.* 28, 113.

Roberts & Roberts (1939). *Soil Sci.* 48, 135.

Thimann, K. V. (1937). *Amer. J. Bot.* 24, 407.

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LATTICE SQUARES

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1. INTRODUCTION

THIS is one of a series of papers describing new methods of analysing quasi-factorial and incomplete block designs. These modified methods of computation have as their object the recovery of the information contained in the inter-block or inter-row and inter-column comparisons. The methods applicable to three-dimensional lattices have been described by Yates (1939), where a full discussion of the principles involved will be found.

The present paper deals with the type of design known as quasi-Latin,' or lattice, squares. This type of design was first described by Yates (1937). In essence it consists of a set of randomized blocks, in which the plots of each block form a square pattern on the ground, certain restrictions being imposed on the randomization within the blocks. These restrictions enable the differences between the rows and columns of each block to be eliminated, either partially or entirely, from the varietal comparisons.

Any lattice square design must contain a number of varieties (or treatments) which is a perfect square, and a design with p^2 varieties requires either $\frac{1}{2}(p+1)$ or $p+1$ replications. With $\frac{1}{2}(p+1)$ replications (which are only possible if p is odd), the design is balanced as far as intra-row and column comparisons are concerned, but the inter-row comparisons only give information on one-half the varietal degrees of freedom, and the inter-column comparisons on the other half. Thus, if inter-row and inter-column information is utilized, and the row and column comparisons are of differing accuracy, as will frequently occur in practice, there will be some difference in accuracy in the comparisons of the adjusted yields, though this difference in accuracy is never likely to be very large.

With $p+1$ replications, on the other hand, information is obtained on every varietal degree of freedom from both row and column comparisons, and consequently all varietal comparisons will be of equal accuracy, even if the row and column comparisons are of differing accuracy.

Table I. *Set of lattice squares for 25 varieties,*
before randomization of rows and columns

Square I					Square II					Square III				
1	2	3	4	5	1	13	25	7	19	1	15	24	8	17
6	7	8	9	10	20	2	14	21	8	18	2	11	25	9
11	12	13	14	15	9	16	3	15	22	10	19	3	12	21
16	17	18	19	20	23	10	17	4	11	22	6	20	4	13
21	22	23	24	25	12	24	6	18	5	14	23	7	16	5

Table I shows a design for 25 varieties with three replications. The structure of the design is such that every variety occurs once and once only with every other variety either in the same row or the same column of one of the squares. The groups of varieties which form the rows and columns of the three squares are in fact the groups given by the rows and columns and the four orthogonal squares of a 5×5 set of orthogonal squares. As far as is known such sets of orthogonal squares only exist when p is a prime or a power of a prime.[1] Thus lattice squares cannot be used for 36, 100 or 144 varieties.

Before laying out any trial on the ground the numbers must be assigned to the varieties (or treatments) at random, the rows of each square must be interchanged in a random order, and the columns must also be similarly interchanged. With $p+1$ replications the second $\frac{1}{2}(p+1)$ replications are obtained from the first $\frac{1}{2}(p+1)$ replications by turning each square through a right angle so as to interchange rows and columns, and then re-randomizing rows and columns as above.

In the original paper only the complete elimination of row and column differences was described. If, however, the actual variation of rows and columns is small, this results in loss of information. In the limiting case when all three sets of comparisons are of equal accuracy, this loss amounts to $1 - E$, where E, the efficiency factor, equals $(p-1)/(p+1)$. The most accurate results can be obtained by determining the actual accuracy of the row and column comparisons relative to the intra-row and column comparisons, and weighting the three sets of comparisons according to their relative accuracy.

It is the object of this paper to describe the computations which are necessary to effect this expeditiously.

[1] Complete sets of orthogonal squares of sides 3, 4, 5, 7, 8 and 9 have been given by Fisher & Yates (1938). Methods of generating sets of larger squares have been given by Stevens (1939).

2. CASE OF $\frac{1}{2}(p+1)$ REPLICATIONS

(a) *Subdivision of varietal comparisons into sets of orthogonal degrees of freedom*

If an orthogonal set of squares of side p exists, then from any p^2 quantities $p+1$ sets of totals can be formed corresponding to the groupings given by the $p-1$ orthogonal squares and the rows and columns of the basic square. Each set will contain p totals, each of p quantities.

If the quantities represent the yields of the p^2 varieties, then corresponding to any variety v there will be $p+1$ totals (one from each set) containing this variety. These totals may be denoted by P_{1v}, $P_{1'v}$, P_{2v}, $P_{2'v}$, ... If G is the total of all the yields and y_v is the yield of variety v, then we have the identity $py_v = P_{1v} + P_{1'v} + P_{2v} + P_{2'v} + \ldots - G$. Consequently instead of estimating the varietal differences directly, we may estimate the differences within each set of totals.

(b) *Estimation of varietal differences*

Now consider a set of $\frac{1}{2}(p+1)$ lattice squares. Let the row total of the row containing varieties $v, v', v'', \ldots$ in the first square be denoted by $_IP_{1v}$, and let the totals of these same varieties in the second, third, etc., squares be $_{II}P_{1v}$, $_{III}P_{1v}$, etc. Similarly let the column total of the column containing variety v in square 1 be denoted by $_IP_{1'v}$, etc.

From the structure of the squares the comparisons represented by P_{1v}, which are confounded with the rows of square I, are completely unconfounded with both rows and columns of the remaining squares. Therefore if w_r is the weight assignable to row comparisons and w_i the weight assignable to intra-row and column comparisons, the most accurate estimate $_wP_{1v}$ of P_{1v} (in units of the total yield of $\frac{1}{2}(p+1)$ plots) is given by

$$_wP_{1v} = \frac{1}{2}(p+1)\{w_r\,_IP_{1v} + w_i(_{II}P_{1v} + _{III}P_{1v} + \ldots)\}/(w_r + \frac{1}{2}(p-1)\,w_i)$$

$$= {}_sP_{1v} + \frac{w_i - w_r}{w_r + \frac{1}{2}(p-1)\,w_i}({}_sP_{1v} - \frac{1}{2}(p+1)\,_IP_{1v}),$$

where $_sP_{1v} = {}_IP_{1v} + {}_{II}P_{1v} + {}_{III}P_{1v} + \ldots$, $_sP_{1v}$ being derivable directly from the ordinary table of varietal totals.

Consequently in the case of a square of side p we have the general expressions

$$_wP_{1v} = {}_sP_{1v} + \lambda L_{1v}$$

for sets confounded with rows, and

$$_wP_{1'v} = {}_sP_{1'v} + \mu M_{1'v}$$

for sets confounded with columns, where

$$L_{1v} = {}_SP_{1v} - \tfrac{1}{2}(p+1)\,{}_IP_{1v}, \quad M_{1'v} = {}_SP_{1'v} - \tfrac{1}{2}(p+1)\,{}_IP_{1'v},$$

$$\lambda = \frac{w_i - w_r}{w_r + \tfrac{1}{2}(p-1)\,w_i}, \quad \mu = \frac{w_i - w_c}{w_c + \tfrac{1}{2}(p-1)\,w_i}.$$

The adjusted total yield of variety v is therefore obtained from the unadjusted total yield by adding quantities

$$\delta_{1v} + \delta_{2v} + \ldots + \epsilon_{1'v} + \epsilon_{2'v} + \ldots,$$

where $\delta_{1v} = \lambda L_{1v}/p$ and $\epsilon_{1'v} = \mu M_{1'v}/p$, etc.

(c) *The analysis of variance*

Rows and columns are not orthogonal with varieties, and this must be taken into account when calculating the sums of squares in the analysis of variance.

As has already been pointed out (1939), the numerical analysis can best be conducted by calculating the sums of squares for rows and columns freed from varietal differences, as this enables direct estimates to be made of the accuracy of the row and column comparisons.

If this is done, and at the same time the sum of squares for varieties is calculated directly from the varietal totals, the intra-block err ir may be obtained by subtraction.

The sum of squares for rows freed from varietal effects is given by the aggregate of the sums of squares of the deviations of each set of L's. The divisor for this sum of squares is $\tfrac{1}{4}p\,(p^2-1)$. The sum of squares for columns freed from varietal effects is obtained similarly.

(d) *Calculation of the relative weights*

The yields, apart from varietal effects, may be regarded as the sum of three quantities normally and independently distributed, the first of which has the same value for all plots of a row, the second of which has the same value for all plots of a column, and the third of which varies from plot to plot. If the variance of the first quantity is A_r, second quantity A_c, and the third B, and there were no varietal effects to be eliminated, the expectation of the mean square for rows in the analysis of variance would be $pA_r + B$. Since the varietal effects corresponding to any set of rows are confounded in one out of $\tfrac{1}{2}(p+1)$ replications, the effect of the elimination of the varietal effects from rows is to reduce this expectation to $p\left\{1 - \dfrac{1}{\tfrac{1}{2}(p+1)}\right\}A_r + B$ or $p\dfrac{p-1}{p+1}A_r + B$. The expectation of the error mean square will be B.

If E_r', E_c' and E_i are the mean squares for rows, columns and error respectively, and we equate these mean squares to their expectations, we have

$$1/w_r = pA_r + B = \{(p+1) E_r' - 2E_i\}/(p-1),$$

and similarly for $1/w_c$. Also $1/w_i = E_i$. We then find

$$\lambda = \frac{2 (E_r' - E_i)}{(p-1) E_r'} \quad \text{and} \quad \mu = \frac{2 (E_c' - E_i)}{(p-1) E_c'}.$$

When E_r' or E_c' is less than E_i, λ or μ, as the case may be, is taken to be zero, since it may be assumed that in no case are the inter-row or inter-column comparisons more accurate than the intra-row and column comparisons.

The determination of the relative weights is necessarily subject to errors of estimation, and this will lead to some loss of accuracy. The point is investigated further in § 6.

When λ and μ have been found, the adjusted yields can be calculated in the manner already indicated.

(e) *Standard errors of the adjusted yields*

Each pair of varieties has either a row in common or a column in common in one of the squares. If there is a row, say, in square 1 in common, the difference of the adjusted total yields is

$$\frac{1}{p}\{(_wP_{2v} - {_wP_{2v'}}) + (_wP_{3v} - {_wP_{3v'}}) + \ldots$$
$$+ (_wP_{1'v} - {_wP_{1'v'}}) + (_wP_{2'v} - {_wP_{2'v'}}) + \ldots\}$$

there being $\frac{1}{2}(p-1)$ differences corresponding to rows, and $\frac{1}{2}(p+1)$ differences corresponding to columns.

The variance of each of the row differences, $P_{2v} - P_{2v'}$, etc., is $\dfrac{\frac{1}{2}p(p+1)^2}{w_r + \frac{1}{2}(p-1) w_i}$, and of each of the column differences is $\dfrac{\frac{1}{2}p(p+1)^2}{w_c + \frac{1}{2}(p-1) w_i}$. Consequently the variance of the difference of the adjusted yields of the two varieties is

$$2 \times \frac{(p+1)^2}{4p}\left\{ \frac{\frac{1}{2}(p-1)}{w_r + \frac{1}{2}(p-1) w_i} + \frac{\frac{1}{2}(p+1)}{w_c + \frac{1}{2}(p-1) w_i} \right\}.$$

If the pair of varieties have a column in common, it is only necessary to interchange w_r and w_c in the above expression.

These two variances cannot differ very greatly, the maximum possible difference being $2/p^2 \times$ the mean variance of a difference. Consequently it will ordinarily be sufficient to take the mean variance as the common

variance of all comparisons. In terms of the quantities already given, this gives the following expression for the standard error of a single adjusted varietal total:

$$\sqrt{\tfrac{1}{2}\,(p+1)\,\{1+\tfrac{1}{2}\,(\lambda+\mu)\}}\ E_t.$$

3. EXAMPLE OF 5×5 LATTICE WITH THREE REPLICATIONS

Table II gives the plan and yields in pounds of sugar of a sugar beet experiment conducted at Woburn in 1939. This was a manurial experiment which included the 25 treatment combinations shown in Table III. As the interactions were of particular interest, it was considered advisable to obtain all comparisons with equal accuracy, instead of adopting the usual procedure of confounding some of the higher order interactions, and a lattice square design was therefore adopted. Each plot was 65·2 links (along rows) by 25 links (along columns). The harvested area of each plot was $\tfrac{1}{75}$ acre.

The steps of the analysis are as follows:

(1) The row and column totals are obtained and entered in Table II, and the treatment totals are also obtained and entered in Table III.

(2) The quantities L and M are calculated and entered in Table II. Thus, for instance,

$$+17\cdot1 = 177\cdot5 + 207\cdot9 + 212\cdot6 + 195\cdot9 + 189\cdot5 - 3 \times 322\cdot1,$$

with the check

$$-251\cdot7 = 4857\cdot9 - 3 \times 1703\cdot2.$$

(3) The analysis of variance is completed as shown in Table IV. The total sum of squares and the sums of squares for squares and treatments are calculated in the ordinary manner. The sum of squares for rows is obtained from the sets of quantities L, with divisor $\tfrac{1}{4} \times 5 \times 24 = 30$, being

$$\tfrac{1}{30}\,(17\cdot1^2 + 25\cdot6^2 + \ldots + 38\cdot1^2 + \ldots + 84\cdot2^2 + \ldots)$$
$$-\tfrac{1}{150}\,(251\cdot7^2 + 104\cdot7^2 + 147\cdot0^2).$$

The sum of squares for columns is similarly obtained from the sets of quantities M. Finally, the error sum of squares is obtained by subtraction, and the mean squares are calculated.

(4) The quantities λ and μ are now calculated as follows:

$$\lambda = \frac{2\,(84\cdot94 - 16\cdot88)}{4 \times 84\cdot94} = 0\cdot4006, \quad \frac{\lambda}{p} = 0\cdot0801,$$

$$\mu = \frac{2\,(26\cdot20 - 16\cdot88)}{4 \times 26\cdot20} = 0\cdot1779, \quad \frac{\mu}{p} = 0\cdot0356.$$

Table II

Square I

	sy	ny	n	sz	s	Total	L	δ
	61·2	67·7	68·1	65·2	59·9	322·1	+17·1	+1·4
	mz	nx	mx	nw	nz			
	69·4	67·4	64·9	77·6	67·7	347·0	+25·6	+2·1
	w	x	c	cy	m			
	46·3	59·7	76·2	80·3	71·2	333·7	−93·7	−7·5
	—	cx	my	cw	mw			
	55·2	77·0	82·4	80·4	77·7	372·7	−120·8	−9·7
	sw	sx	z	y	cz			
	73·9	79·0	51·6	44·8	78·4	327·7	−79·9	−6·4
Total	306·0	350·8	343·2	348·3	354·9	1703·2		−20·1
M	−39·2	−53·1	−40·3	−82·3	−36·8		−251·7	
ε	−1·4	−1·9	−1·4	−2·9	−1·3	−8·9		

Square II

	mz	y	c	s	cx	Total	L	δ
	69·1	49·6	72·6	68·7	74·0	334·0	−38·1	−3·1
	cw	n	nx	w	cz			
	62·7	74·0	78·1	40·0	66·3	321·1	+3·8	+0·3
	ny	nz	sw	my	cy			
	68·9	78·1	69·6	68·1	68·5	353·2	+20·1	+1·6
	m	—	sz	sx	mx			
	64·7	38·6	57·4	65·5	67·1	293·3	+60·5	+4·9
	z	x	mw	nw	sy			
	48·0	39·0	64·9	72·2	58·7	282·8	+58·4	+4·7
Total	313·4	279·3	342·6	314·5	334·6	1584·4		+8·4
M	+23·9	+11·0	+10·2	+22·7	+36·9		+104·7	
ε	+0·9	+0·4	+0·4	+0·8	+1·3	+3·8		

Square III

	sy	my	nx	y	m	Total	L	δ
	57·6	69·2	64·0	31·8	58·4	281·0	+84·2	+6·8
	nz	sz	z	w	cx			
	72·2	73·3	46·2	45·9	73·4	311·0	−16·7	−1·3
	sx	mz	cy	mw	n			
	61·4	77·9	73·1	70·4	70·5	353·3	+ 9·9	+0·8
	c	cz	—	ny	nw			
	58·6	68·4	46·7	71·3	69·1	314·1	+45·5	+3·6
	cw	x	s	mx	sw			
	56·6	52·9	60·9	71·8	68·7	310·9	+24·1	+1·9
Total	306·4	341·7	290·9	291·2	340·1	1570·3		+11·8
M	+89·3	−28·4	+34·5	+9·5	+42·1		+147·0	
ε	+3·2	−1·0	+1·2	+0·3	+1·5	+5·2		

Grand total = 4857·9

The quantities L are multiplied by λ/p to give the δ's, and the quantities M by μ/p to give the ϵ's, which are entered in Table II.

(5) The adjusted total yields are then calculated by adding to each

unadjusted total yield the appropriate δ's and ϵ's, six in all. Thus the adjusted total yield of the unmanured plots is

$$140\cdot5 - 9\cdot7 - 1\cdot4 + 4\cdot9 + 0\cdot4 + 3\cdot6 + 1\cdot2 = 139\cdot5.$$

The standard error of each total is given by

$$\sqrt{[3 \times \{1 + \tfrac{1}{2}(0\cdot4006 + 0\cdot1779)\} \times 16\cdot88]} = 8\cdot08.$$

These yields have finally to be converted to cwt. per acre by multiplying by the conversion factor $0\cdot2232$. The converted yields are shown in Table VIII.

Table III. *Treatment totals*

	Nil	Nitrate of soda (n)	Calcium nitrate (c)	Sulphate of ammonia (s)	Muriate of ammonia (m)
Nil —	140·5	212·6	207·4	189·5	194·3
Pot. chloride (w)	132·2	218·9	199·7	212·2	213·0
Sod. chloride (x)	151·6	209·5	224·4	205·9	203·8
Pot. sulphate (y)	126·2	207·9	221·9	177·5	219·7
Sod. sulphate (z)	145·8	218·0	213·1	195·9	216·4

It is worth noting that in spite of the additional restrictions that have been imposed on the randomization the experiment can be validly analysed as if it were one in ordinary randomized blocks, the error sum of squares being simply the difference of the total sum of squares and the sums of squares for squares (blocks) and treatments in Table IV. This analysis gives the error appropriate to the unadjusted treatment totals. In this example the standard error is $\sqrt{(3 \times 36\cdot22)} = 10\cdot42$.

Table IV. *Analysis of variance*

	D.F.	Sum of squares	Mean square
Squares	2	426·33	213·16
Rows, eliminating treatments	12	1019·26	84·94
Columns, eliminating treatments	12	314·34	26·20
Treatments, ignoring rows and columns	24	7346·68	306·11
Error	24	405·04	16·88
Total	74	9511·65	

Since $10\cdot42^2/8\cdot08^2 = 1\cdot66$, the gain in efficiency resulting from the adjustment, attributable to the use of lattice squares instead of ordinary randomized blocks, is 66 % (excluding losses due to errors in weighting, discussed in § 6). In other words, to attain results of the same accuracy by the use of ordinary randomized blocks five replications would have been required instead of three.

Had the original method of complete elimination of rows and columns

been followed, the standard error of an adjusted treatment total would have been

$$\sqrt{(3 \times 16 \cdot 88 \times 6/4)} = 8 \cdot 72.$$

The gain in information over ordinary randomized blocks would therefore have been $10 \cdot 42^2/8 \cdot 72^2 - 1$ or 43%.

4. Case of $(p+1)$ replications

(a) *Estimation of varietal differences*

When there are $(p+1)$ replications the row and the column comparisons each give information on all the varietal degrees of freedom. It is therefore possible, by applying the inverse of the process outlined in § 2 (a), to construct estimates of the varietal differences from the row totals only, and from the column totals only. If $_ry_v$ and $_cy_v$ represent these estimates (in terms of the total yield of each variety), and $S(R_v)$ and $S(C_v)$ are respectively the sums of all the row and column totals containing variety v, then

$$p\,_ry_v = (p+1)\,S(R_v) - G, \quad p\,_cy_v = (p+1)\,S(C_v) - G.$$

The factor $(p+1)$ has to be included since each set of comparisons given by the row totals is based on only one of the $p+1$ replications.

If $_uy_v$ is the unadjusted estimate of the total yield of variety v, and $_iy_v$ is the estimate based on intra-row and column comparisons only, we have

$$_uy_v = S(y_v) = \{_ry_v + _cy_v + (p-1)\,_iy_v\}/(p+1).$$

The weighted estimate $_wy_v$ is therefore given by

$$_wy_v = \frac{w_r\,_ry_v + w_c\,_cy_v + (p-1)\,w_i\,_iy_v}{w_r + w_c + (p-1)\,w_i}$$

$$= _uy_v + \frac{w_i - w_r}{w_r + w_c + (p-1)\,w_i}\,(_uy_v - _ry_v) + \frac{w_i - w_c}{w_r + w_c + (p-1)\,w_i}\,(_uy_v - _cy_v)$$

$$= _uy_v + \frac{\lambda'}{p}\,L_v' + \frac{\mu'}{p}\,M_v',$$

where

$$L_v' = p\,(_uy_v - _ry_v) = p\,S(y_v) - (p+1)\,S(R_v) + G,$$

$$M_v' = p\,(_uy_v - _cy_v) = p\,S(y_v) - (p+1)\,S(C_v) + G,$$

$$\lambda' = \frac{w_i - w_r}{w_r + w_c + (p-1)\,w_i}, \quad \mu' = \frac{w_i - w_c}{w_r + w_c + (p-1)\,w_i}.$$

(b) *The analysis of variance*

The sum of squares for rows freed from varietal but not column effects is given by the sum of squares of the quantities L_v' already obtained, the divisor being $p^3(p+1)$, and similarly the sum of squares for columns freed from varietal but not from row effects is given by the sum of squares of the quantities M_v'.

In order to complete the analysis of variance it is also necessary to form estimates of the row differences freed from both varietal and column differences. In terms of our previous notation the row differences of square I (in terms of totals of p plots) are given by the differences of the p quantities

$$_\text{I}P_{1v} - \frac{1}{p-1}\left(_\text{II}P_{1v} + _\text{III}P_{1v} + \ldots + _\text{II'}P_{1v} + _\text{III'}P_{1v} + \ldots \right).$$

These sets of differences can be combined in just the same manner as were the row totals. The total of $(p-1)$ times all the quantities corresponding to rows containing variety v (with sign reversed) will be found to be

$$J_v = p\, S(y_r) - p\, S(R_v) - S(C_v) + G.$$

The sum of squares of these p^2 quantities will give the sum of squares for rows freed from both varietal and column effects, the divisor being $p^3(p-1)$.

Similarly the sum of squares for columns freed from varietal and row effects is obtained from the quantities

$$K_v = p\, S(y_v) - S(R_v) - p\, S(C_v) + G.$$

We can therefore construct the analysis of variance table either by including rows eliminating both varieties and columns, and columns eliminating varieties only, or by including rows eliminating varieties only, and columns eliminating both rows and varieties. In practice it is best to calculate both sets of sums of squares, as these provide a useful check with very little extra labour.

(c) *Calculation of the relative weights, etc.*

In adjusting the row differences of any one square, so as to free them from varietal effects without introducing any column effects, there are $p-1$ squares available for determining the varietal effects, since in the remaining square the varietal effects involved are confounded with columns. Consequently the expectation of the mean square for rows, eliminating varieties and columns, is reduced from $pA_r + B$ to $(p-1)A_r + B$.

Equating this expectation to the actual mean square E_r', we find

$$w_r = \frac{p-1}{pE_r' - E_i}.$$

Similarly

$$w_c = \frac{p-1}{pE_c' - E_i},$$

and $w_i = 1/E_i$.

As before, if E_r' or E_c' is less than E_i, w_r or w_c may be taken to be equal to w_i.

Nothing is gained by substituting for w_r, w_c and w_i in the expressions for λ' and μ', which are best evaluated by first determining w_r, w_c and w_i.

The standard error of the adjusted total yields is

$$\sqrt{(p+1)(1+\lambda'+\mu')}\, E_i.$$

5. EXAMPLE OF 5×5 LATTICE WITH SIX REPLICATIONS

An experiment similar to that described in § 3, but with six replications, was carried out at Rothamsted in 1939. To save space the plan and the individual plot yields, and also some of the details of the computations, have not been reproduced here, but Tables V and VI give the necessary totals from which the remainder of the analysis can be completed.

Table V. *Treatment totals*

	n	c	s	m
—	297·3	341·7	351·5	330·9	358·0
w	289·4	356·4	362·1	333·2	344·7
x	292·9	363·9	366·5	334·7	354·1
y	308·7	363·9	338·3	341·1	330·4
z	283·5	369·7	359·0	349·6	357·9

Table VI. *Sums of row and column totals*

$S(R_v)$

	—	n	c	s	m
—	1691·2	1677·1	1691·5	1661·1	1745·1
w	1640·4	1709·5	1773·8	1723·8	1693·3
x	1673·5	1694·2	1750·3	1628·7	1679·0
y	1721·0	1735·1	1687·1	1677·9	1660·0
z	1619·7	1761·9	1722·4	1688·9	1690·5

$S(C_v)$

	—	n	c	s	m
—	1644·2	1711·3	1734·1	1712·9	1722·1
w	1649·3	1716·7	1710·4	1659·1	1650·4
x	1687·2	1762·8	1729·5	1676·2	1739·2
y	1670·9	1684·4	1682·6	1720·2	1688·3
z	1651·7	1677·3	1696·4	1701·5	1718·3

The steps of the analysis are as follows:

(1) The row and column totals of each square are entered in the original table of yields in their appropriate positions.

(2) The treatment totals, and the totals of all the row totals containing a given treatment, and of all the column totals containing a given treatment, are obtained. These are shown in Tables V and VI. Thus the totals of the rows containing the untreated plots in the six squares are 258·1, 277·4, 291·7, 278·1, 302·5 and 283·4, giving a total of 1691·2.

As a good deal of the labour involved in the construction of these tables consists of locating the plots having the given treatment, it is worth while to form all three totals simultaneously. This can be done on an ordinary calculating machine by shifting the carriage.

(3) The quantities L', M', J and K can now be calculated. To facilitate this calculation it is worth tabulating the differences D of the sums of the row totals and the sums of the column totals. The four quantities can then be computed successively with great rapidity. The calculation for the no fertilizer treatment proceeds as follows:

$$D_0 = S(R_0) - S(C_0) = 1691·2 - 1644·2 = +47·0,$$
$$L_0' = 5S(y_0) - 6S(R_0) + G = 5 \times 297·3 - 6 \times 1691·2 + 8479·4 = -181·3,$$
$$J_0 = L_0' + D_0 = -181·3 + 47·0 = -134·3,$$
$$K_0 = J_0 + 4D_0 = -134·3 + 4 \times 47·0 = +53·7,$$
$$M_0' = K_0 + D_0 = +53·7 + 47·0 = +100·7,$$

with the check

$$M_0' = 5 \times 297·3 - 6 \times 1644·2 + 8479·4 = +100·7.$$

The numerical values of L', M', J and K are set out in four tables of 25 values each, similar to Tables V and VI. The sum of all the values in each of these four tables should be zero.

(4) The analysis of variance is next completed, as shown in Table VII. The total sum of squares and the sums of squares for squares and treatments are calculated in the ordinary manner. The sum of squares for rows, eliminating varieties, is given by the sum of the squares of all the values of L', with divisor $5^3 \times 6 = 750$. The sum of squares for columns, eliminating varieties, is similarly obtained from the values of M'. The sum of squares for rows, eliminating varieties and columns, is obtained from the values of J, with divisor $5^3 \times 4 = 500$, and the sum of squares for columns, eliminating varieties and rows, from the values of K. In no case is there any correction to be deducted from these sums of squares, since each set of values has zero total.

Finally the error sum of squares is obtained by subtraction, including either rows eliminating varieties only, and columns eliminating both varieties and rows, or alternatively rows eliminating both varieties and columns, and columns eliminating varieties only. This provides a valuable check.

<div align="center">Table VII. Analysis of Variance</div>

	D.F.	Sum of squares	Mean square
Squares	5	350·28	70·06
Rows, eliminating treatments	24	1074·43	44·77
Rows, eliminating treatments and columns	24	1036·58	43·19
Columns, eliminating treatments	24	664·95	27·71
Columns, eliminating treatments and rows	24	627·10	26·13
Treatments, ignoring rows and columns	24	2658·03	110·75
Error	72	915·55	12·72
Total	149	5625·39	

(5) The quantities w_r, w_c, w_i, λ' and μ' are then calculated as follows:

$$w_r = \frac{4}{5 \times 43\cdot19 - 12\cdot72} = 0\cdot01968,$$

$$w_c = \frac{4}{5 \times 26\cdot13 - 12\cdot72} = 0\cdot03392,$$

$$w_i = 1/12\cdot72 = 0\cdot07862,$$

$$w_i - w_r = 0\cdot05894, \quad w_i - w_c = 0\cdot04470, \quad w_r + w_c + 4w_i = 0\cdot36808,$$

$$\lambda' = 0\cdot1601, \quad \tfrac{1}{5}\lambda' = 0\cdot03202,$$

$$\mu' = 0\cdot1214, \quad \tfrac{1}{5}\mu' = 0\cdot02428.$$

(6) The adjusted total yields are calculated by multiplying L' and M' by λ'/p and μ'/p respectively, and adding these corrections to the unadjusted total yields. Thus for the no fertilizer treatment the adjusted yield is

$$297\cdot3 + 0\cdot03202 \times (-181\cdot3) + 0\cdot02428 \times (+100\cdot7) = 293\cdot9.$$

The standard error of each adjusted yield is given by

$$\sqrt{\{6 (1 + 0\cdot1601 + 0\cdot1214) 12\cdot72\}} = 9\cdot89.$$

The yields are then converted to cwt. per acre (conversion factor 0·1339), these converted yields being shown for both experiments in Table VIII.

There is no need to discuss the results of the experiments in detail here. The responses to the mineral salts were only small, and consequently it is not to be expected that any very striking interactions with the

nitrogenous fertilizers will be revealed. A small response to the mineral fertilizers containing sodium is shown in both experiments, and reaches significance in the Woburn experiment. Nitrate of soda is also the best of the nitrogenous fertilizers in both experiments, being significantly better than sulphate of ammonia at Rothamsted and both sulphate of ammonia and calcium nitrate at Woburn. The only apparent interaction between the mineral and nitrogenous fertilizers is a depression with potash salts in the absence of nitrogen at Woburn. ·

Table VIII. *Adjusted yields, cwt. per acre, Rothamsted and Woburn*

	Rothamsted						Woburn					
	—	Sod. nitr.	Calc. nitr.	Amm. sulph.	Amm. chl.	Mean	—	Sod. nitr.	Calc. nitr.	Amm. sulph.	Amm. chl.	Mean
—	39·4	46·0	46·9	44·6	46·8	44·8	31·1	48·1	45·2	42·5	44·6	42·3
Pot. chl.	39·2	47·7	47·1	44·4	47·3	45·2	27·5	51·0	43·2	46·8	46·5	43·0
Sod. chl.	38·4	48·4	48·1	46·8	47·6	45·8	33·1	48·7	47·1	46·3	47·5	44·6
Pot. sulph.	40·0	48·9	45·7	45·7	45·0	45·1	27·1	47·3	48·3	43·2	48·4	42·8
Sod. sulph.	38·7	49·3	48·1	47·3	48·4	46·4	32·0	49·7	46·8	44·1	47·9	44·1
Mean	39·1	48·1	47·2	45·7	47·0	45·4	30·2	49·0	46·1	44·6	47·0	43·4
St. error			1·32						1·80			

If the Rothamsted experiment is analysed as if it were one in ordinary randomized blocks, the standard error of an unadjusted treatment total is found to be 11·44. Thus the gain in efficiency resulting from the adjustment, attributable to the use of lattice squares instead of ordinary randomized blocks, is 34 %. In other words, to obtain results of the same accuracy by the use of ordinary randomized blocks, eight replications would have been required instead of six.

Had the original method of complete elimination of rows and columns been followed, the standard error of an adjusted treatment total would have been 10·70. The gain in information over ordinary randomized blocks would therefore have been 14 %. The new method of adjustment has therefore resulted in a further gain of about 18 %, less errors due to inaccuracies of weighting, which, as shown in the next section, are not likely to be more than about 3 %.

6. LOSS OF INFORMATION DUE TO INACCURACIES OF WEIGHTING

Since the relative weights are estimated from somewhat small numbers of degrees of freedom, it is important to ascertain whether the loss of information due to inaccuracies of weighting is so great as to nullify the gain in accuracy resulting from the weighting.

In the case of $\frac{1}{2}(p+1)$ replications the degrees of freedom confounded

with rows may be considered separately from those confounded with columns. We then obtain the following general expression for the percentage loss of information on the comparisons confounded with either rows or columns

$$\frac{(2\rho+1)\,(F-1)^2}{\{(2\rho+1)\,F-1\}^2+2\rho},$$

where ρ is the ratio of the true intra-row and column weight to the true inter-row or inter-column weight, and F is distributed as is e^{2z} with $\frac{1}{2}(p^2-1)$ and $\frac{1}{2}(p-3)(p^2-1)$ degrees of freedom.

For any given value of ρ a series of values of this expression may be calculated, corresponding to the various probability levels of the F distribution. For probability levels which would give $w_i < w_r$ or $w_i < w_c$ the value of F which gives $w_i = w_r$ or $w_i = w_c$ is taken. The average loss of information may then be obtained by numerical integration over the whole probability scale.

The case of $p=5$ with three replications has been worked out, the following losses of information being obtained:

ρ	1	2	4	6	8	12
Mean percentage loss	2·52	4·04	4·02	3·14	2·53	1·81

These losses must be set off against the gains resulting from the use of the lattice squares. If the amount of information obtained from ordinary randomized blocks of 25 plots is taken as a 100 units, we obtain the following table of values for the net amount of information obtainable from the use of lattice squares:

ρ	1	2	4	6	8	12
Information with known weights	100·0	111·1	150·0	192·6	236·1	324·1
Loss due to inaccuracies of weights	2·5	4·5	6·0	6·1	6·0	5·9
Net information	97·5	106·6	144·0	186·5	230·1	318·2

It thus appears that even in a set of three 5×5 lattice squares, where only 12 degrees of freedom are available for estimating the accuracy of the row or column comparisons, the loss of information due to inaccuracies of weighting is by no means sufficiently great to outweigh the advantages of the lattice design. With a larger number of replications, or with larger squares, the loss of information from this cause will be quite trivial.

SUMMARY

A new method of analysing the results of experiments arranged in lattice (quasi-Latin) square designs is described. By this method the information contained in the inter-row and inter-column comparisons

is recovered. The procedure followed is to estimate the actual accuracy of the inter-row and inter-column comparisons relative to intra-row and column comparisons, and assign weights proportional to these relative accuracies.

The methods of computation by which this procedure can be carried out expeditiously are described in detail, and are illustrated by two experiments carried out at Rothamsted and Woburn. The gains in accuracy obtained in these two experiments (as compared with ordinary randomized blocks) were approximately 30% and 60% respectively, allowing for losses of information due to inaccuracies of weighting.

These gains have been obtained without any additional field work, the only extra work being that required in drawing up the arrangement and in analysing the results. Moreover, if for any reason the additional statistical analysis cannot be undertaken, or does not appear to be worth while, lattice square experiments can be validly analysed just as if they were arrangements in ordinary randomized blocks.

It appears, therefore, that the use of lattice squares is likely to be of considerable value in variety trials involving large numbers of varieties, especially in those cases where ordinary Latin squares are found to be ineffective in reducing the variability of the experimental material.

REFERENCES

FISHER, R. A. & YATES, F. (1938). *Statistical Tables for Biological, Agricultural and Medical Research.* Edinburgh: Oliver and Boyd.
STEVENS, W. L. (1939). *Ann. Eugen., Lond.,* **9**, 82–93.
YATES, F. (1937). *Ann. Eugen., Lond.,* **7**, 319–31.
—— (1939). *Ann. Eugen., Lond.,* **9**, 136–56.